

AN ABSTRACT OF THE THESIS OF

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in Botany and Plant Pathology presented on October 12, 1990.

Title: Organic Pesticide Modification of the Species Interactions in an Annual Plant Community.

Redacted for Privacy

Abstract approved:

Donald Zobel

The impact on natural plant communities from the release of organic chemicals into the atmosphere, both as applied pesticides and industrial waste products, is not well understood. In order to study the potential impacts in a reasonable time, plant communities were established using soil containing the seed bank from an annually plowed field that had had no pesticide application for over ten years. The communities were grown in raised beds producing a community area of 0.8 m². Atrazine, 2,4-D and malathion were applied at two concentrations, at or below the manufacturers' recommended level except the high malathion treatment, with all treatments done in triplicate. Measurements were made on eight major species, as well as effects of interspecific competition on two target species. Cover by species was monitored over time in nested neighborhoods of 10 cm and 20 cm around individuals of Poa annua and Calandrinia ciliata. Neighborhood biomass and total community biomass were harvested after all species began flowering.

Community production decreased with atrazine and 2,4-D treatments, but not with malathion. All tested compounds modified species abundance. The most notable effect was the alteration of dominance and the simplification in communities treated with atrazine and 2,4-D and, to a lesser extent, malathion. There were four general response patterns exhibited by a species' biomass in treated communities: it 1) decreased, 2) increased, 3) was unaffected or 4) decreased only at the high concentration. In one significant exception, Erodium was equally reduced by malathion at both concentrations. Organic chemicals altered interspecific competitive relations for all treated communities. Chemical treatment changed the identity of consistently competitive species (i.e., species significant in at least three of four sampling times) and the timing of interactions. Each target species had its own suite of competitors that individually changed with chemical treatment. Ten cm neighborhoods had more competitive interactions than the 20 cm neighborhood, when cover was used as a predictor of competitive influence. However, when biomass was used, the 20 cm neighborhood accounted for more interactions. Neighborhood cover was a more useful predictor of target biomass than final neighborhood biomass, because it was simple to use, indicated more species interactions, and was nondestructive. This use of artificial plant communities to study the effects of organic chemicals is simple and economical, and the experiments generate small amounts of contaminated waste. The method also uses naturally occurring plants, which is uncommon under current federal regulations, but reduces the environmental heterogeneity common in most field studies. The method is amenable to transport and is appropriate for studying other processes in plant communities.

Organic Pesticide Modification of the Species Interactions
in an Annual Plant Community

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed October 12, 1990

Commencement June 1991

APPROVED:

Redacted for Privacy

Professor of Botany in charge of major

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Date thesis is presented October 12, 1990

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ACKNOWLEDGEMENTS

As with any project there are many more people involved than are listed on the title page. I thank all those that have helped me and I apologize to those that I have unintentionally forgotten.

The help of my committee was instrumental in the completion of this project. Donald Zobel, my advisor, provided patience, helpful suggestions and sensitivity. Mark Wilson added his statistical expertise and advice on ecological questions. Steven Radosevich introduced me to the practical applications of plant ecology and an encouraging group of graduate students, in particular Bruce Maxwell. Bruce provided insightful discussions on plant competition, graduate school and mountain biking.

The Environmental Protection Agency has supported this work in its entirety. Harold Kibby was instrumental in initiating that support. Craig Mc Farlane, who has been my supervisor, has encouraged me at the expense of his own projects and his counsel has been greatly appreciated.

Walt Guetter and Scott Schroeder helped build and move the raised beds. Ray Shimabuku and Jim Dray helped fill them with soil. Carolyn, Amanda, and Adam Pfleeger assisted in plant sorting during the 1988 season. Donald Stufflebeam and Somvong Tragoonrung (Sam) help sort the 1989 season plants. Recinda Sherman periodically helped with a variety of tasks including data entry and proofing. Mike McDowell introduced me to SAS (maybe I should not thank him). Stu Eide, Rosemary Owens, and Ted Ernst have all contributed computer assistance

that has been greatly appreciated. Ray Shimabuku, my office partner for almost ten years, helped in many ways including his own sick humor. The use of his bicycle, the 'Rolls', which is such a piece of junk that it no longer needs to be locked, saved me invaluable time going to classes and other appointments on campus.

A special thanks goes to my wife, Carolyn who supported me emotionally through the ups and downs of this whole process. Her reality therapy was necessary.

Thank you all.

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ORGANIC PESTICIDE MODIFICATION OF THE SPECIES INTERACTIONS IN AN ANNUAL PLANT COMMUNITY

INTRODUCTION

Reports by the Superfund Amendments and Reauthorization Act of 1986 indicate that over one billion kilograms of toxic air pollutants were released into the atmosphere of the United States in 1987 (US EPA, 1989). This is the first quantitative report on the amounts of air toxicants released. It is considered to be a conservative estimate, because some companies did not report and some sources were not required to report (e.g. small manufacturers and users, and federal facilities) (Poje et al., 1989; US EPA, 1989). Other sources of organic toxins include over 500 million kilograms of pesticide (Pimental and Levitan, 1986), of which an estimated one percent reaches target organisms (Pimental and Edwards, 1982), and 500 million kilograms of creosote, petroleum and coal tar products produced annually in the United States (Pimental and Levitan, 1986).

While most toxic air pollutants have unknown phytotoxic properties, eighty-five percent of pesticides applied are herbicides (USDA, 1987). Sixty-five percent of pesticides are applied aurally (US ASCS, 1976) with almost 50 percent of applications missing the targeted agriculture land (Ware et al., 1970). The majority of pesticides is lost to adjoining ecosystems while some remains in the atmosphere or volatilizes back into the atmosphere (Thompson, 1983), which may be deposited in distant ecosystems (Pimental and Edwards, 1982).

The detection and measurement of low concentrations of organic chemicals in the atmosphere is difficult, due to the lack of adequate analytical techniques (e.g.

Rice et al., 1985). When found, concentrations in rainfall are generally nanograms per liter of rainwater (Strachan, 1988), while concentrations in fog are thousands of times higher (Glottfelty et al., 1987). Fog exposes the entire plant surface and some organic residues become more concentrated on the surface as moisture evaporates (Glottfelty et al., 1987). In general, anthropogenic compounds are ubiquitous in the world environment (Strachan, 1988), although concentrations are highest near sources and decline with distance (Rice et al., 1985; Richards et al., 1987). Pesticides have been detected even in remote areas such as Pacific islands (Atlas and Giam, 1981) and the arctic (Paasivirta et al., 1985), as well as agricultural (Rice et al., 1985) and urban (Bruckmann et al., 1988) areas.

Terrestrial plant communities receive chronic exposure to hundreds of different organic chemicals. Dramatic changes in plant community composition have been produced by such air pollutants as oxidants (Hayes and Skelly, 1977; Miller, 1973), sulfur dioxide (Winterhalder, 1984; Legge, 1980), and fluoride (Bunce, 1979). The environmental significance of organics is unknown, but forest decline in Europe and eastern North America may in part be the result of anthropogenic and biogenic hydrocarbons (Foster, 1989; Krahel-Urban et al., 1988).

Traditionally, toxicologists have used single species tests to determine toxicity of a compound. These methods do not develop data necessary to understand effects at the community level. In particular, effects upon species interactions cannot be predicted with such tests. This type of information is considered more important since the 1981 report to the National Research Council (Cairns et al., 1981) on testing the effects of chemicals on ecosystems. Single species phytotoxicity tests have

historically used agricultural plants, species that have little or no relation to the highly variable natural plant populations that are being exposed. While data on xenobiotic impact on community composition and abundance will lead to useful conclusions, information is also needed on changes in processes such as competition, which will help make reasonable predictions on the consequences of using a particular toxicant.

Low concentrations of organic chemicals were used in this study to 1) develop a methodology for studying their effects on plant communities, 2) determine their influence on community composition and abundance in model plant communities, and 3) determine their effects on interspecific competition.

There are several other related questions to be addressed, both from a biological and a regulatory viewpoint. Specifically, are other parameters that are easier to quantify, such as community biomass, equally good indicators of the modification of competitive patterns? When using the neighborhood approach to study plant competition, can the size of the sphere of influence (neighborhood diameter) be predicted or determined in order to avoid excessive measurement? If the goal is only to determine if competitive relations are altered, does it matter what target species is used? And, finally, is there evidence that community level testing is a better indicator of non-target phytotoxicity than single species testing?

LITERATURE REVIEW

PLANT COMPETITION

Plant competition is an area of intense study and controversy and even its definition has provoked discussion. Clements' et al. (1929) definition, that competition begins when the immediate supply of a single necessary factor falls below the combined demand of the plants, was one of the earliest. Grime (1979) expanded on this definition to state that competition was the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space. Competition has also been defined as the induction of strain in one organism as a result of the use, defense, or sequestering of resources by another organism (Welden and Slauson, 1986). Welden and Slauson (1986) subdivided competition into an intensity component, the amount of strain that competition induces in an organism, and an importance component, the relative degree that competition contributes to the overall decrease of the growth rate, metabolism, fecundity, survival or fitness of an organism below its optimal condition. Competition has also been subdivided into effect and response components, where effect is the ability of an organism to reduce the performance of another organism and response is the ability of an organism to perform relatively well in the presence of competition (Goldberg and Fleetwood, 1987).

There are four major methodologies used to study plant competition: additive, substitutive, systematic and neighborhood experiments (Radosevich, 1987). Additive experiments generally use a crop species held at a constant density and another species, generally a weed, planted at a variety of densities. The substitutive

method has a constant density of plants but the ratio between plant species changes. Substitutive methods overcome the problem of changing densities in additive experiments, but do not have predictive abilities needed to determine effects at different densities. Systematic methods vary both density and species ratios. This overcomes the deficiencies of both additive and substitutive methods. These three methods have been restricted mainly to agricultural and forestry applications, for which the mean crop yield is important. However, in natural systems mean yields of a population have little ecological or evolutionary significance. Rather, the response of the individual to its environment is more important in making ecological or evolutionary projections. Neighborhood experiments take this approach, evaluating the response of an individual (target) based on its surrounding biotic and abiotic environment (neighborhood).

The neighborhood methodology is based on the concept that plant competition is a spatial process in which differences in growth rates are generated by a disproportionate sharing of available resources among plants, depending on the number of competitive neighbors, their proximity and their relative sizes (Bonan, 1988). Most methods for studying plant interference use density as a measure to summarize the biotic environment of the target. However, density is a crude measure of the state of the population or conditions met by the individuals (Mack and Harper, 1977), and may obscure important variation. Individual plants interact primarily with nearby plants, so density-dependent population dynamics in plant communities are perhaps best understood in terms of spatially local interactions that affect individual performance (Pacala, 1986). Natural selection operates at the level

of the individual and the vigor and abundance of individuals within a population appear to be a complex function of the age and spatial arrangement of its members (Mack and Harper, 1977). Plants do not react to density *per se* but to the proximity and performance of neighbors, with target performance being a function of the neighbors' conditions, such as their size, distance, number, age, genotype and angular dispersion (Weiner, 1984).

Neighborhood studies using annual plants have also been instrumental in understanding the mechanisms underlying size inequality (size hierarchies) in plant populations, the importance of symmetric and asymmetric competition, and coexistence of apparent competing species.

Size inequality, a prevalent feature of plant populations, has been reported in even- and mixed-age stands and in single and multi-species communities (Gerber, 1989). Annuals have been used to determine the processes forming size inequalities because they generally germinate and die synchronously, lack clonal growth, lack root grafting and their response to interference is consistently plastic (Mack and Harper, 1977). Numerous hypotheses have been published to account for size inequalities, including effects of emergence time, genetic variability in relative growth rate, microhabitat variation, seed size, seed dormancy, herbivores, parasites, cotyledon size and retention time, density, maternal effects, and competition (Mack and Harper, 1977; Watkinson et al., 1983; Silander and Pacala, 1985; Pacala and Silander, 1985; Weiner, 1985; Weiner and Thomas, 1986; and Firbank and Watkinson, 1987). The role of competition in size inequalities in plant populations would be important if a) asymmetry of mass distribution were greater in the

presence of competition and b) distribution of masses would be more variable in the presence of competition (Turner and Rabinowitz, 1983). Turner and Rabinowitz (1983) concluded that dominance and suppression (competition) were not responsible for size inequality in their experiment, but rather inequality was the result of the variability in exponential growth rates. However, Weiner and Thomas (1986) reported that in 14 out of 16 experiments competition did cause size inequalities, but only when competition was asymmetric.

Two sided or symmetric competition occurs for nutrients or water, which are shared resources and are divided in proportion to the relative masses of the individuals (Bonan, 1988). Symmetric competition reduces relative growth rate of all individuals by the same proportion, so it is generally not a factor producing size inequalities in plant populations (Weiner and Thomas, 1986). In asymmetric or one sided competition, the larger individual receives most of the resource, such as light (Bonan, 1988; Weiner, 1986). Formation of size inequality is generally an expression of the genetic variation among plants in growth rates, which is enhanced by neighborhood competition (Bonan, 1988). Asymmetric competition for light is the competitive factor most likely responsible for increasing size inequalities (Weiner and Thomas, 1986; Weiner, 1986, Miller and Weiner, 1989; and Gerber, 1989).

The coexistence of different plant species within a similar habitat has been addressed by neighborhood analysis using annuals. Both dispersal distance and strength of inter- and intraspecific competition have significant impacts on coexistence. Short dispersal distances may help lead to long-term coexistence because it induces interspecific spatial segregation (Harper, 1977; Pacala, 1986). If

interspecific competition is more intense than intraspecific competition and competition is local, then stable coexistence of two competing species is possible (Weiner and Conte, 1981). When the above conditions are met, then species may acquire territories from which other species are excluded and the sets of patches can be in equilibrium (Weiner and Conte, 1981).

Several techniques have been developed to evaluate the importance of neighborhood effects on target individuals, including polygon, regression and other model building techniques. Polygon analysis starts with a polygon being drawn around the target individual, with the sides halfway between the target and adjacent neighbors. In some cases, the distance has been weighted so that larger individuals receive more of the distance between plants than do smaller individuals. Polygon analysis has accounted for up to 59 percent of the variation in carrot size (Mead, 1966). When seedling polygon areas were compared to polygon areas of mature plants at harvest, early neighborhood establishment was more important in determining final dry weight of Lapsana at harvest ($R^2 = .60$ to $.30$) (Mithen et al., 1984). In contrast, polygon area or number of plants had less effect on plant survival than did cotyledon opening time when sunflowers were the test species. Also, only a small percent of sunflowers that died as a result of self thinning had small polygon areas (Watkinson et al., 1983). Polygon analysis has been criticized for taking into account only adjacent neighbors (Silander and Pacala, 1985).

The most common method to evaluate neighborhood experiments has been linear regression analysis. Mack and Harper (1977) found that between 32 and 69 percent of the variation in target biomass could be accounted for by the biomass,

distance and angular dispersion of the neighbors (Mack and Harper, 1977). Others have used density and time of emergence to account for 50 percent of the variance in plant yield (Firbank and Watkinson, 1987) or neighborhood radius and angular dispersion to account for 70 percent of the variation in seed set (Silander and Pacala, 1985). Waller (1981) used number, size and angular concentration of neighbors to account for 5-59 percent of the variation in leaf number on herbaceous perennials. A major problem with using regression in neighborhood studies is the potential use of individuals both as targets and neighbors for adjacent targets, thereby violating the assumption of independence of samples required by normal distribution theory (Mitchell-Olds, 1987).

While linear regression models have been popular, other models have also been successful, especially hyperbolic models. A hyperbolic model was used with distance and number of individuals accounting for between 83-86 percent of the variation in peduncle number in two species of knotweed (Weiner, 1982). Goldberg and Fleetwood (1987) accounted for 79 percent of the variance in target weight of four annuals with a hyperbolic function of the weight or the density of neighbors. Hyperbolic models have theoretical support in that they imply that the quantity of resources that would otherwise be gathered by a solitary plant is divided among itself and its neighbors. Linear models, in contrast, imply that each neighbor takes a fixed quantity of resources from a focal point and thereby fail to account for plasticity of neighbors' growth (Pacala and Silander, 1987).

Neighborhood studies have also been evaluated by using skewness (Turner and Rabinowitz, 1983), and Gini coefficients (Weiner and Thomas, 1986) and

analyzed with path analysis (Mitchell-Olds, 1987). The logical step from examining data using such methodologies is to build models that have predictive abilities. Weiner and Conte (1981) developed a model incorporating adults, seeds, seed dispersal and local neighborhood competition that suggests that spatial heterogeneity of populations can arise and be maintained through local competition and dispersal when interspecific competition is more intense than intraspecific competition. More sophisticated dynamic population models based on linking neighborhood sub-models concerning survivorship, fecundity, dispersal and germination have led to an understanding of the important determinants of the dynamics and structure of plant communities (Pacala and Silander, 1985; Pacala, 1987). These dynamic models have indicated at least three types of relations among spatial scales that may be important. These are interactions between the scale of spatial heterogeneity in the physical environment, mean seed dispersal distance and the distance over which nearby plants interact (neighborhood radii) (Pacala, 1987).

PHYTOTOXICITY

Testing of chemical toxicity to terrestrial plants in the United States has been driven by the Toxics Substances Control Act (TSCA)(15 U.S.C. 2601 et seq.) of 1976 and the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA)(7 U.S.C. 136 et seq.) of 1978, which can require phytotoxicity tests for registration and reregistration prior to the release of chemicals into the environment. Under both TSCA (40 CFR part 797) and FIFRA (40 CFR part 158), a tiered approach is used: the amount of testing depends on the phytotoxicity of the compound (tier

1, least, to tier 3, most toxic). Prior to chemical registration, TSCA may require a seed germination/root elongation test, and an early seedling growth toxicity test (tier 1 and 2) and a plant uptake and translocation test (tier 3), for ten agricultural species (Table 1). Field testing has not been required. Under FIFRA, tier 1 and 2 require two plant tests for ten angiosperm species, a seed germination/seedling emergence test and a vegetative vigor test. Tier 1 tests use one concentration; tier 2 tests use five. Tier 2 testing is required if an EC_{25} occurs in tier 1 testing (EC_{25} = effective concentration that reduces a measured parameter to 25% of controls). Tier 3 testing is required if the maximum recommended rate or anticipated environmental exposure is greater than the EC_{25} for one or more species from tier 2. Tier 3 uses a field test in which three dicotyledons, three monocotyledons, two vascular cryptogams, one bryophyte or hepatophyte and one gymnosperm, all from different families, are grown under conditions similar to the natural or agricultural habitat.

EPA also has suggested phytotoxicity testing (Green et al., 1989) under the Comprehensive Environmental Response Compensation and Liability Act (CERCLA) as amended by Superfund Amendments and Reauthorization Act of 1986 (SARA) (42 U.S.C. 9601 et seq.). Recommended terrestrial plant tests are a 120 hour static seed germination test and a 120 hour static root elongation test using lettuce. These tests are used to assess biological toxicity at superfund sites.

The only other federal agency that routinely requires plant testing is the FDA (Food and Drug Administration), under the authority of the National Environmental Policy Act of 1969 (NEPA). Their major concern is food chain contamination via soil amendments and additives to livestock feeds. Their

Table 1. Species that are required or suggested for use in phytotoxicity tests. RUBI = Rubinstein et al., 1975. Acronyms are defined in the phytotoxicity section of the literature review.

PHYTOTOXICITY TEST

SPECIES	COMMON NAME	RUBI	TSCA ¹	FIFRA ²	FDA ³	OECD ⁴
MONOCOTS						
<u>Allium cepa</u>	onion		X			
<u>Avena sativa</u>	oats	X	X		X	X ^A
<u>Lolium perenne</u>	ryegrass	X	X		X	X ^A
<u>Oryza sativa</u>	rice					X ^A
<u>Sorghum bicolor</u>	sorghum					X ^A
<u>Triticum aestivum</u>	wheat				X	X ^A
<u>Zea mays</u>	corn	X	X	X	X	
DICOTS						
<u>Brassica alba</u>	mustard					X ^B
<u>B. campestris</u>	chinese cabbage					X ^B
<u>B. napus</u>	rape					X ^B
<u>B. oleracea</u>	cabbage		X		X	
<u>B. rapa</u>	turnip					X ^B
<u>Cucumis sativus</u>	cucumber	X	X		X	
<u>Daucus carota</u>	carrot		X		X	
<u>Glycine max</u>	soybean		X	X	X	
<u>Lactuca sativa</u>	lettuce		X		X	X ^C
<u>Lepidium sativum</u>	cress					X ^C
<u>Lycopersicon esculentum</u>	tomato	X	X		X	
<u>Phaseolus aureus</u>	mung bean					X ^C
<u>P. vulgaris</u>	bean	X			X	
<u>Raphanus sativus</u>	radish					X ^B
<u>Trifolium ornithopodioides</u>	fenugreek					X ^C
<u>T. pratense</u>	red clover					X ^C
<u>Vicia sativa</u>	vetch					X ^C

¹ Other species of economic or ecological importance may also be used. Ten species minimum.

² Ten species. Six dicot species from at least four families. One must be soybean and a second must be a root crop. Four monocot species from at least two families. One must be corn.

³ Four species; two monocots and two dicots, one of which is a legume.

⁴ Three species must be used, one from each group X^A, X^B, and X^C.

procedures (FDA, 1987) require a seed germination/root elongation test and a seedling growth test similar to those required by EPA under TSCA (Table 1).

The Organization for Economic Co-operation and Development, an international organization headquartered in France, recommends a growth test that uses a modified native soil in pots and three species, one grass, one crucifer and one from a group mainly composed of legumes (Table 1) (OECD, 1981).

From the regulatory standpoint, "nonagricultural" plant species are not emphasized; community level tests are not suggested even under the more stringent FIFRA guidelines. This is true despite a EPA report (Rubinstein et al., 1975) that noted the lack of information on chemical effects in natural plant communities. Guderian and Kueppers (1980) added that it was probably not justifiable to transfer dose-effect relationships determined from agroecosystems, with generally favorable conditions, to natural ecosystems. Responses of plant communities to low dosages of air pollutants, for example, effects on interspecific competition, were almost totally unknown. Since the 1975 report there have been few publications on phytotoxicity in natural habitats and those have been limited to only a few taxa (Fletcher et al., 1988).

The few studies involving the ecotoxicological effects of organic chemicals in plant communities have investigated the impacts associated with vegetation control on rights-of-way (Marshall, 1988; Spencer et al., 1988), agriculture (Hume 1987, 1988), old fields (Suttman and Barrett, 1979; Tomkins and Grant, 1974; Malone, 1972; Barrett, 1968) and on occasion, after accidents causing environmental degradation (Kershaw and Kershaw, 1986; Belsky, 1975). While these reports are

of scientific value, they do not present a systematic way of evaluating potential ecological impacts of pollutants. Multi-species or community level tests are needed; the 1981 report of the National Research Council (Cairns et al., 1981) documented the inadequacy of single-species toxicity testing. Single-species tests have five deficiencies in predicting ecosystem responses (Pontasch et al., 1989). Single-species tests 1) ignore interactions among species, 2) use genetically homogeneous laboratory-stock test populations that lack the adaptive capability of heterogeneous natural populations, 3) use species of unknown relative sensitivities, 4) are often conducted under physical and chemical conditions different from natural habitats, and 5) use species that are usually not indigenous to the ecosystem, thus complicating field validation of the test.

While these reasons may seem sound, especially to an ecologist, multi-species testing is very controversial, in particular in the regulatory community. Kimerle (1986) suggests that there is no justifiable reason always to rely upon, or default to, more complicated and costly ways of arriving at environmental safety decisions when laboratory derived toxicity data are adequate when used with the safety concept of hazard assessment. Slooff (1985) recommended against multi-species testing in routine hazard evaluation, due to its lack of sensitivity, and stated that single species test predictions are reliable. In contrast, Perez and Morrison (1985) in the same book concluded that single-species and multispecies testing were equally cost effective. It has even been suggested that whole ecosystem manipulation may be a useful mechanism for discerning community and ecosystem impacts of toxicants (Perry and Trvelstrup, 1988). When single-species tests were compared to

community level tests, the single species tests were not successful in predicting the exact nature of the community level effects, in particular effects due to altered interspecies interactions (Hansen and Garton, 1982).

While multi-species testing may never replace single-species testing, it has additional benefits: the potential to 1) identify species interactions, 2) illustrate chemical-physical pathways, 3) calibrate and verify mathematical models of ecosystems, 4) assess population-, community-, and ecosystem-level response to toxicants, 5) elucidate mechanisms and interactions, 6) study functioning ecosystems with cybernetic or negative feedback loops in place, 7) identify sensitive or critical species to be used in single-species tests, and 8) test hypotheses (Dickson et al., 1985). Before terrestrial multi-species testing is to become a functional methodology, improvements are required. "Community Toxicity Testing" (ASTM, 1986) lists no terrestrial plant tests and only one terrestrial test; all other existing multispecies and/or community level tests are aquatic.

TEST CHEMICALS

Atrazine

General information - Atrazine is a preplant, pre-emergent or post-emergent triazine herbicide that has been used extensively since its development in the early 1950s (Knusli, 1970). Atrazine is the second most used pesticide in the United States (40 million kg) (Gianessi, 1988), while in Oregon in 1987 it was the third most used herbicide and the sixth most used pesticide (263,000 kg). Its use in Oregon has more than doubled since 1981, with the majority of the increase attributed to grass

seed crops and to a lesser extent corn (Rinehold and Witt, 1989). The herbicide is non-toxic to bees and has an acute toxicity (LD_{50}) in rats of 1780 mg/kg (Sine, 1989). It is used as a selective herbicide in corn, sorghum, sugar cane, macadamia orchards, pineapple and turf grass (Sine, 1989; WSSA, 1983). It is also used in conifer reforestation, Christmas tree plantations and the non-selective control of vegetation in fallow fields. Atrazine degrades rapidly in soil and generally rotational crops can be planted one year following application. Cold and arid or semi-arid conditions can slow or reduce its degradation in soil (WSSA, 1983).

Atrazine is applied using a water carrier and absorbed most effectively through the root. The herbicide is translocated acropetally via the apoplastic system and accumulates in apical meristems and leaves, where it inhibits the Hill reaction in photosynthesis, curtailing electron transfer from Q to the plastoquinone pool (Ebert and Dunford, 1976). Lethal concentrations of atrazine induce water-soaked lesions beginning near leaf margins or veins; chlorosis follows, then leaf necrosis and death. These symptoms occur more rapidly than could be accounted for by lack of photosynthate. Death may result from a secondary phytotoxic agent, protective carotinoid related reactions, and/or photooxidative pigment destruction (Ashton and Crafts, 1981).

Secondary effects - Temperature, light availability and humidity all can change the rate of absorption, translocation and detoxication of atrazine and, hence, the plants' tolerance. Sub-lethal effects can include increased uptake of nutrients, increasing shoot growth and higher protein and carbohydrate content, while decreasing root growth. Atrazine probably interferes with auxin and cytokinin action

in roots (Ebert and Dunford, 1976). Atrazine has also been reported to reduce tensile strength of centipedegrass sod (Turner and Dickens, 1987). Seed germination or dormancy may be inhibited, stimulated, or unaffected depending on environment and concentration (Ebert and Dunford, 1976).

Simazine, a relative of atrazine, increased the nutrient content (particularly nitrogen) of plants, increasing the severity of many plant diseases (Griffiths, 1981). Application of atrazine decreased resistance to maize dwarf mosaic virus in corn (MacKenzie et al., 1964) and increased the inoculum potential of Fusarium in peas and corn (Percich and Lockwood, 1975).

Metabolism - The three major pathways of atrazine metabolism are hydrolysis, dealkylation and glutathione conjugation (Esser et al., 1975; Shimabukuro et al., 1971a). The dechlorination by hydrolysis to 2-hydroxy atrazine contributes to detoxification but is not essential for atrazine resistance. This pathway is more important when atrazine is absorbed through the roots, particularly with corn (Shimabukuro et al., 1971b). The 2,N-dealkylation seems to be universal in organisms, and to be responsible for intermediate resistance found in peas and cotton (Shimabukuro et al., 1971a). Glutathione conjugation is the major pathway of metabolism in resistant plants such as sugar cane, corn, sorghum and Johnson grass (Jensen, 1982). Glutathione-s-transferase controls the amount of detoxification and therefore the selectivity of triazine herbicides in higher plants. Any or all atrazine degradation pathways may be present in resistant plants. However, atrazine resistance in certain weed species is not due to atrazine degradation (Radosevich and Holt, 1982); resistant weeds change their thylakoid membrane composition with

atrazine present, which allows electron transport to continue.

2,4-D

General information - 2,4-D is a chlorinated phenoxy herbicide with a LD_{50} in rats of 375 mg/kg (Sine, 1989). It was developed during World War II and soon became widely used in agriculture. It is a selective, hormone-type herbicide used on grasses, grains, sugar cane, and noncrop areas for broadleaf control (Sine, 1989; WSSA, 1983). Its phytotoxic properties persist from 1-4 weeks in warm moist soil. 2,4-D can be applied to post-emergent vegetation as a spray, using water or diesel as a carrier. While roots absorb the salt (polar) form, leaves more readily absorb the ester (nonpolar) form. Regardless of point of uptake, the chemical is translocated symplastically and accumulates near shoot and root meristems. 2,4-D causes dedifferentiation and initiation of cell division in certain mature cells, and inhibits cell division in primary meristems. In meristematic regions, abnormal growth responses affect respiration, food reserves, and cell division, but the primary mode of action has not been established (WSSA, 1983). Nucleic acid metabolism and cell wall plasticity are relevant to the mechanism of action (Ashton and Crafts, 1981).

Nationally, 2,4-D is the fourth most used pesticide (20.5 million kg) (Gianessi, 1988). In Oregon it is the most used herbicide and the fourth most used pesticide statewide (376,000 kg). Use has declined from a high of over 590,000 kilograms in the late 1950's. It has been replaced in many cases with sulfonyleurea herbicides (Rinehold and Witt, 1989).

Secondary effects - At low concentrations, 2,4-D acts as a plant growth regulator, inducing rooting and blossom set. It controls ripening of bananas and citrus fruits, and can delay fruit dehiscence (WSSA, 1983). Undesirable secondary responses were reported as early as 1947, when 2,4-D application to sugar cane resulted in a four-fold increase in cane borers (Ingram et al., 1947). Often increases in insect and disease damage occur: examples include insects of wheat (Fox, 1948), peas (Maxwell and Harwood, 1960), rice (Ishii and Hirano, 1963), corn (Oka and Pimentel, 1974) and oats (Adam and Drew, 1969) and plant diseases of wheat (Purdy, 1967), corn (Oka and Pimentel, 1974), tomatoes (Sinha and Wood, 1967; Rowell, 1953), and tobacco (Simons and Ross, 1965). Shifts in soil invertebrate populations have also been reported (Webster, 1967). The balance between competing diseases can shift when 2,4-D application decreases sugar content in leaves (Griffiths, 1981). For example, target spot (low sugar fungus) on tomatoes increased while rust infections (high sugar fungus) decreased (Griffiths, 1981). 2,4-D effects on insect infestation and disease have not been investigated for nontarget species.

Metabolism - The metabolism of 2,4-D is less understood than that of atrazine. Three major routes of metabolism are oxidation of the acetic side chain, hydroxylation of the aromatic ring, and conjugation with plant constituents. None of these can conclusively account for differential sensitivity among plant species (Naylor, 1976; Loos, 1975). Resistant species seem to lack responsive sites or require high concentrations at those sites. These species generally lack a vascular cambium and pericycle tissue (Hanson and Slife, 1969).

Malathion

General information - Malathion is a general purpose insecticide used to kill chewing and sucking insects on fruits and vegetables, by contact, vapor action or as a stomach poison (Matsumura, 1975). Malathion was the first organophosphorus insecticide with high selective toxicity. The carboxyl ester group is readily hydrolyzed by mammalian carboxesterase in the liver (Eto, 1974). The LD₅₀ in male rats is 1375 mg/kg (Sine, 1989), higher than for 2,4-D. Due to its low mammalian toxicity and high insecticidal activity it has been used extensively by the World Health Organization for anopheles eradication (Eto, 1974). Malathion is one of the twenty most used pesticides in the United States (1.1 million kg) (Gianessi, 1988). In Oregon it is tied with chlorpyrifos as the second most used insecticide behind oil, with an estimated use in 1987 of 73,000 kg (Rinehold and Witt 1989).

Secondary effects - There is little information on phytotoxicity of insecticides. However, malathion was the most phytotoxic insecticide tested by Clower and Matthyse (1954). The other ten insecticides they tested were all chlorinated hydrocarbons, many now banned in the United States. Malathion caused phytotoxic damage (chlorosis and leaf edge scorch) to vegetable crops and ornamentals (Dennis and Edwards, 1962) when applied at five times the normal rate. It killed cucumber at this concentration (Dennis and Edwards, 1961). The most phytotoxic insecticides tested by Dennis and Edwards were DDT, aldrin, dieldrin (chlorinated hydrocarbons), ROGOR, TEPP, and malathion (organophosphates). Malathion caused a loss of pollen viability for over fourteen days in cabbage. Lal (1975) attributed this to the delicate nature of anthers and a physiologically selective site.

This suggests the possibility of decreased reproduction by plants exposed to malathion. Zelena (1977) found increased nitrogen levels in leaves sprayed with malathion. This could change the pathogen balance as occurs with atrazine, but there are few reports of insecticides reducing plant disease resistance (Griffiths, 1981).

Metabolism - Little work has been done on the metabolism of malathion in vascular plants. The three major pathways in animals (Matsumura, 1975) are hydrolysis, oxidation and carboxylation. Hydrolysis eliminates the methane side chain. Oxidation replaces one sulfur atom with oxygen. While oxidation commonly produces malaoxon, it is not responsible for the differential sensitivity to malathion in animals and oxidation is not responsible for malathion degradation in plants (Rowlands, 1965). Malathion resistance is determined by the amount of carboxylesterase activity; plants have carboxylesterase (Rowlands, 1964), which may explain their general resistance to malathion.

METHODS

PLANT MATERIALS AND CONDITIONS

The plant species were gathered as seeds in soil from the Oregon State University Botany and Plant Pathology Farm located just east of Corvallis, Oregon. The field containing the seeds has been disturbed annually for over ten years with no direct application of agricultural fertilizers or pesticides (Lewis Tate, personal communication, 1986). The disturbance, any combination of plowing, discing or rototilling beginning in the late spring and continuing intermittently to early fall, prevented plants from maturing during the summer and therefore selected for winter annuals. The site is used by plant taxonomy classes to study plants typical of fallow fields in the Willamette Valley of Oregon.

Soil containing the seed bank was collected from the top 5 cm of the field in the late summer of 1987 and 1988, when aboveground vegetation was absent. The soil was sieved through a 6 mm screen and mixed with a commercial potting soil (Promix) in a 50:50 ratio by volume in the fall of 1987 and a 40:60 ratio in the fall of 1988. Promix prevented the farm soil from hardening and diluted the seed density.

Fifteen raised beds were constructed from 2 x 8 inch Douglas-fir lumber. They enclosed an inside volume of 0.6 m high and 0.9 m square with a soil block of 0.49 m³. The beds were sufficiently high to minimize root interactions from adjacent vegetation. The beds were located outside at the U.S. EPA Western Fish Toxicology Station, approximately 2 km south of Corvallis. The wooden frames were filled to within 5 cm of the top with unfertilized bulk soil or 'garden loam',

purchased locally. The 'garden loam' was irrigated and covered to enhance the germination of its seed bank. Seedlings were destroyed with a propane torch, a method chosen to minimize soil disturbance. Osmocote fertilizer (14-14-14) was added at a rate of 126 g/m² to the top of the garden loam in 1987. This was not done in the fall of 1988 because fertilization caused excessive growth in certain species, making it difficult to harvest individual plants. Therefore, the results from the spring of 1988 were influenced by fertilizer and the 1989 results were much less so. The 'garden loam' was next covered with 1.5 cm of the seed bank soil mixture. The beds were irrigated when the peat in the 'Promix' appeared dry. Irrigation continued until the fall rains began. The beds were watered for the last time on October 26 in 1987 and on October 17 in 1988.

The 12 most common plant species that emerged from the seed bank represent eight families (Table 2); most are widely distributed throughout the United States and other parts of the world.

CHEMICAL TREATMENT

Three agricultural chemicals, atrazine, 2,4-D and malathion (Table 3), were selected as treatments, based on their widespread use in the United States and the large amount of published research that has been done with these chemicals. Chemical treatments were randomly assigned to beds, in triplicate. The fall, 1987, atrazine experiment was set up in a randomized block design; subsequent analysis indicated that blocking had little effect and it was discontinued in 1988 with the 2,4-and malathion experiments. The chemicals were applied after plants had emerged and were less than five cm tall. During chemical application, all beds

Table 2. Plant species that were most abundant in the artificial plant communities. Nomenclature follows Hitchcock et al. (1969).

FAMILY	SPECIES	COMMON NAME	CODE
Asteraceae	<u>Sencio vulgaris</u> L.	groundsel	SEVU
Brassicaceae	<u>Capsella bursa-pastoris</u> (L.) Moench	shepherd's purse	CABU
	<u>Draba verna</u> L.	whitlow grass	DRVE
Caryophyllaceae	<u>Cerastium viscosum</u> L.	annual mouse-eared chickweed	CEVI
	<u>Spergula arvensis</u> L.	spurry	SPAR
	<u>Stellaria media</u> (L.) Cyrill	chickweed	STME
Geraniaceae	<u>Erodium cicutarium</u> (L.) L'Her	filaree	ERCI
Labiatae	<u>Lamium purpureum</u> L.	red dead-nettle	LAPU
Poaceae	<u>Poa annua</u> L.	annual bluegrass	POAN
	<u>Poa bulbosa</u> L.	bulbous grass	POBU
Portulacaceae	<u>Calandrinia ciliata</u> (R. & P.) DC.	red maids	CACI
Scrophulariaceae	<u>Veronica persica</u> Poir.	creeping speedwell	VEPE

Table 3. Composition, source and properties of the three organic chemicals used as treatments.

	ATRAZINE ¹	2,4-D ²	MALATHION ³
Chemical formula	C ₈ H ₁₄ ClN ₅	C ₁₆ H ₁₆ Cl ₂ O ₃	C ₁₀ H ₁₉ O ₆ PS ₂
Manufacturer	Ciba-Geigy	Albaugh	Helena
Product name	AAtrex 80W	Lo-Vol 4D	CYthion
Recommended application rate	2.5 lbs / acre	2 pts / acre	2 pts / acre
Percent of recommended rate used	low = 8% high = 16%	low = 10.6% high = 106%	low = 106% high = 1060%
Actual chemical application rate	low = 16.7 mg/m ² high = 33.4 mg/m ²	low = 8.2 ul/m ² high = 81.9 ul/m ²	low = 81.9 ul/m ² high = 819.3 ul/m ²
Dates of application	Nov 3, 1987	Nov 18, 1988 Nov 29, 1988	Nov 18, 1988 Nov 29, 1988

¹ 2-chloro-4-ethyl-amino-6-isopropylamino-s-triazine

² isooctyl ester of (2,4-dichlorophenoxy) acetic acid

³ o,o-dimethyl dithiophosphate of diethyl mercaptosuccinate

were covered with black plastic except the one receiving treatment. The treatments were applied using a hand held sprayer (Chapin model #2001) in order of increasing chemical concentration, with water as the carrier. The control beds received an equal amount of carrier (water) as did the treatments. In 1988, rain for several days after chemical application required that the treatments be reapplied.

PARAMETERS MEASURED

Poa annua and Calandrinia ciliata were chosen as target species due to their resistance to atrazine, high relative abundance, and taxonomic dissimilarity. Target individuals of the two species were chosen for neighborhood analysis using randomly selected coordinates and a portable grid. The individual of the desired species closest to the coordinates became the target. Ten individuals of each species per bed were chosen. No targets were located within a 10 cm buffer zone around the outside of each soil block.

Percent cover was measured using nested circular quadrats with diameters of 10 and 20 cm, centered on the target individuals. For cover measurements, plant parts that grew into the neighborhood were included and plant parts that grew outside the neighborhood were excluded. The proportion of the neighborhood covered by each species was recorded. Total cover equaled 100 percent and included bare ground. This technique allowed for the repeated nondestructive sampling of the same neighborhoods. Percent cover was measured four times (beginning on January 7, February 23, March 15, April 5) in 1988 and four times in 1989 (beginning on January 10, February 29, March 27, and April 27). Cover

measurements took approximately three days to complete for each sampling date.

Following the final cover measurements each year, all the target individuals were harvested along with six (1989) or seven (1988) 10 and 20 cm neighborhoods per bed. All plants rooted within the neighborhood were harvested at the soil surface. The reference (control) beds were not harvested in 1988 due to the intertwining of the vegetation, especially Stellaria, which made it impossible to trace the plants back to their rooting origin. Plants were sorted by species, dried to constant weight at 60° C, and weighed.

Total biomass of each bed was determined after the neighborhoods had been harvested. Plants were cut at the soil surface, sorted, and processed as the neighborhood biomass measurements. Total biomass was determined by summing the biomass within the neighborhoods plus the biomass remaining in the bed after the neighborhood harvest.

ANALYSIS

Statistical analysis were performed using the Statistical Analysis System (SAS Institute Inc., 1985). The aboveground biomass and cover data were analyzed using a one-way analysis of variance (ANOVA) procedure with a protected LSD (least significant difference) multiple range test ($\alpha \leq 0.05$, $N = 9$, $N = 90$ respectively). The biomass data were log transformed. The ANOVA and multiple range test were used to determine if differences existed among treatments by species for each chemical. The cover data were analyzed separately for each target and sampling period. There was no attempt to statistically compare the data between sampling

periods. In order to analyze changes between sampling periods, means of the cover data ($N = 60$) from the 20 cm neighborhoods of both targets for each treatment were plotted and examined.

Means were calculated for target biomass for each species in each treatment. An ANOVA using a protected LSD multiple means test was used to determine if differences existed between treatments in target performance ($\alpha \leq 0.05$, $N = 90$).

Cover data used in the multiple regression analysis were transformed using the square root of the arcsin of each value. The regression analysis was performed on each treatment at each sampling period ($\alpha \leq 0.1$ and 0.05 , $N = 30$). The log transformed final aboveground biomass of the target species was the response variable and the transformed cover values of each species within either the 10 or 20 cm neighborhoods were the predictor variables [$\log \text{biomass} = f(\arcsin \text{cover})$]. The full model ($y = \beta_0 + \beta_1 x_1 \dots \beta_8 x_8$, where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc.) was used, even though some species were not significant to the model. This was done so that different treatments could be compared. All true outliers (not mistakes) remained in this data set because these one or two individuals, in a data set of 30, were the largest target individuals. If the large individuals had been removed for the sake of a higher R^2 or better residual plots, the most important reproductive individuals in the community would not have been considered. Regression coefficients were used to evaluate interspecific competition: A species was considered to be a consistent competitor if it was significant in the model ($\alpha \leq 0.1$) for at least three of the

four sample times. Following the work of Weldon and Slauson (1986), the importance of competition was determined by the magnitude of R^2 in the regression analysis.

Another set of regression analyses was performed using the final aboveground biomass of neighbors at harvest as independent variables. These analyses were done in a similar manner. Response variables were either the target flower height or the inverse of the target species biomass at harvest. The predictor variable was the log transformed aboveground biomass of each species [$1/\text{biomass} = f(\log \text{neighbor biomass})$] or [$\text{target flower height} = f(\log \text{neighbor biomass})$] within either 10 or 20 cm neighborhoods ($\alpha \leq 0.1$ or 0.05 , $N = 21$ in 1988 and 18 in 1989).

RESULTS

BIOMASS

Total biomass of the plot decreased with increasing atrazine application in 1988. The total aboveground biomass at harvest was significantly reduced ($P=.024$) by the high concentration treatment (Figure 1). The low treatment did not differ significantly from either the control or the high treatment. The individual species constituting the communities demonstrated four distinct patterns of biomass change when treated with atrazine (Figure 1). Stellaria biomass decreased with increased chemical application. Veronica and Lamium biomass was significantly reduced only at the high dose. Calandrinia, Capsella, and Erodium demonstrated no significant change in biomass. However, two of these species, Calandrinia and Capsella, showed a non-significant biomass increase with increasing levels of atrazine. Finally, biomass of both Poa species, the major monocots of the community, increased with an increase in dose.

When 2,4-D was applied in 1989, the resulting communities had significantly less biomass than the controls ($P=.036$) (Figure 1). However, there was no significant difference between the low and high treatments. A two fold increase in atrazine reduced biomass to 77 percent of the lower treatment whereas a tenfold increase of 2,4-D reduced it to 88 percent of the low treatment level.

The species responded differently to 2,4-D than to atrazine treatment (Figure 1). Stellaria, Veronica, and Lamium showed no change in response to application of 2,4-D. However, biomass of Calandrinia, Capsella, and Erodium all decreased with an increased application of chemical. Capsella's response occurred only with

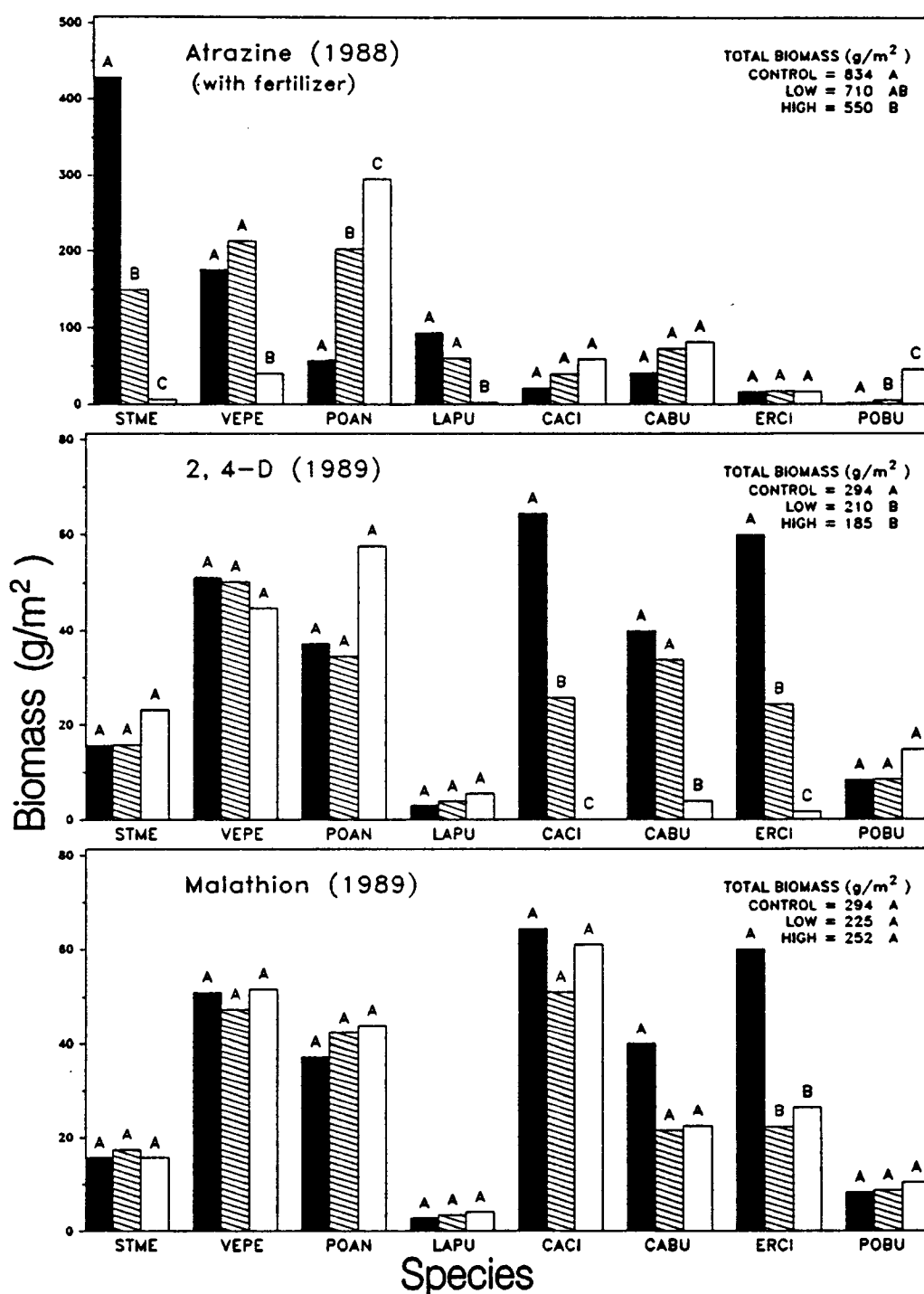


Figure 1. Above-ground biomass at harvest. Treatments: ■ -control ▨ -low □ -high. Species codes are defined in Table 2. Within each species, treatments with the same letter do not differ statistically. Statistically significant differences among treatments were identified using a protected LSD on log transformed biomass data ($\alpha = .05$, $N = 9$).

the high treatment level. Although neither Poa species had a statistically significant difference among treatments ($P=.090$ and $.463$), both produced the greatest biomass in the high treatment.

Malathion caused no significant decrease in community production (Figure 1) ($P=.192$), even at five times the recommended dose. Erodium was the only species that decreased in biomass ($P<.0001$), reacting even at the low dose. Capsella showed a similar pattern, but it was not significant due to the large amount of variability between replicate communities.

The total above-ground biomass in 1988, when all treatments received fertilizer, was approximately 2.5 times that when no fertilizer was applied (1989).

COVER

Percent cover was measured around each target plant (including the target) in both 10 and 20 cm diameter neighborhoods. Changes in community cover values were determined by combining the percent cover in the 20 cm neighborhoods of both targets. Each treatment was represented by the mean of 60 measurements, 20 from each of three replicate communities.

Additionally, a one-way ANOVA was used to determine if differences existed within a species between treatments at each sampling time. Only the results of 20 cm neighborhoods are presented here, because there were only minor differences between the two neighborhood sizes. Each treatment was represented by the mean of 30 measurements, ten from each of three replicate communities. Cover patterns differed by species, chemical treatment, and sampling time, with greater changes in

atrazine and 2,4-D treatments.

Atrazine - The atrazine control treatment started with Stellaria as the dominant species, but by the second sampling period it was a co-dominant (species having similar high amounts of cover) with Lamium and Veronica (Figure 2). At the fourth sampling, Stellaria was again dominant, due in part to completion of Lamium's life cycle. Poa, Calandrinia and Capsella remained understory species for the duration of the experiment except in the fourth sampling period, after Capsella bolted, penetrated the canopy, and increased its cover.

At the low application rate of atrazine, Stellaria, the initial dominant, lost dominance to Veronica and, to a lesser extent, Lamium (Figure 2). Stellaria returned as a co-dominant as Lamium completed its life cycle before the fourth sampling. The other three species remained in the understory for the duration of the experiment.

The high treatment caused a radical change in how the community was structured (Figure 2). Two species dominant in the control and low application treatments, Stellaria and Lamium, were killed. Their death and the low coverage of Veronica led to a community dominated by Poa, Capsella and Calandrinia, the three species forming the understory in the control and low treatment communities.

Increasing atrazine treatment in Poa annua neighborhoods produced significantly higher cover values of Poa, Calandrinia, and Capsella (Table 4). This pattern was established at the first sampling and remained until the end of the experiment for Poa and Calandrinia. However, with Capsella, the low treatment changed from not being significantly different from the control for the first two samplings to being not significantly different from the high treatment by the fourth.

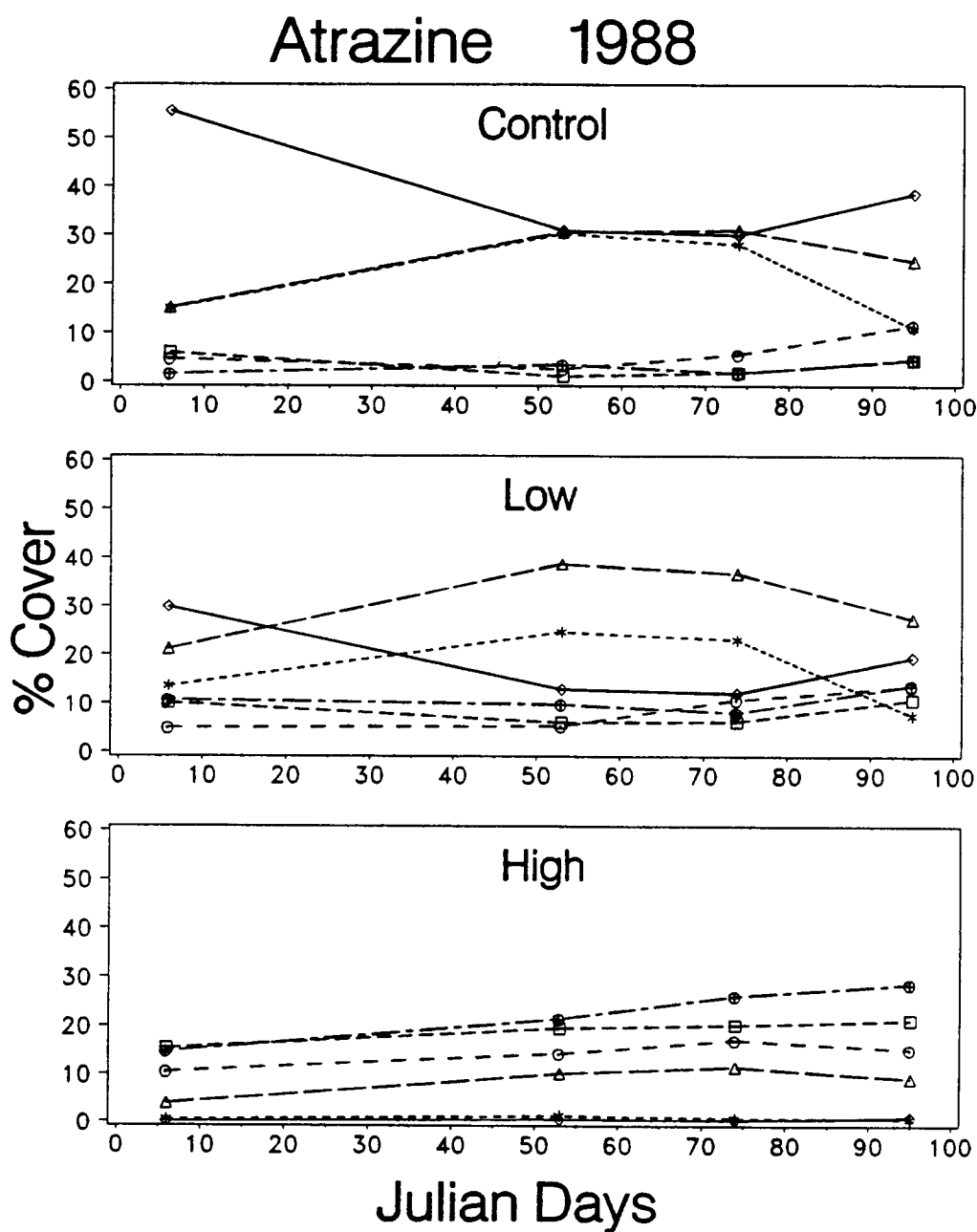


Figure 2. Percent cover over time of the six species with the highest cover values for the 1988 experiment using atrazine. The data are from 20 cm diameter neighborhoods. Each symbol is the mean of 30 samples, 10 from each of three replicate communities. Species: ◇ -STME △ -VEPE * -LAPU ⊙ -POAN and POBU □ -CACI ○ -CABU. Species codes are defined in Table 2. Julian days are from the beginning of the calendar year.

Table 4. Significance of treatment differences for cover within species and sampling times, for atrazine in 1988, using a protected LSD ($\alpha \leq .05$, $DF = 87$). The data are from 20 cm diameter neighborhoods around each of two target species. A = largest mean value, C = smallest mean value. Treatments with the same letter are not significantly different. Species codes are defined in Table 2.

TARGET= <u>Poa annua</u> NEIGHBORHOOD=20 cm circle									
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CACI	CABU	ERCI	BARE GROUND
Control	1	A	B	C	A	C	B	B	C
Low Atrazine	1	B	A	B	B	B	B	A	B
High Atrazine	1	C	C	A	C	A	A	AB	A
Control	2	A	B	C	A	C	B	B	B
Low Atrazine	2	B	A	B	B	B	B	AB	B
High Atrazine	2	C	C	A	C	A	A	A	A
Control	3	A	A	C	A	C	C	B	B
Low Atrazine	3	B	A	B	B	B	B	AB	B
High Atrazine	3	C	B	A	C	A	A	A	A
Control	4	A	A	C	A	C	B	A	B
Low Atrazine	4	B	A	B	B	B	A	A	B
High Atrazine	4	C	B	A	C	A	A	A	A

TARGET= <u>Calandrinia ciliata</u> NEIGHBORHOOD=20 cm circle									
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CACI	CABU	ERCI	BARE GROUND
Control	1	A	B	C	A	B	A	A	C
Low Atrazine	1	B	A	B	A	B	B	A	B
High Atrazine	1	C	C	A	B	A	A	A	A
Control	2	A	B	C	A	C	A	B	B
Low Atrazine	2	B	A	B	B	B	B	B	B
High Atrazine	2	C	C	A	C	A	A	A	A
Control	3	A	B	C	A	B	C	A	B
Low Atrazine	3	B	A	B	B	B	B	A	B
High Atrazine	3	C	C	A	C	A	A	A	A
Control	4	A	B	C	A	C	A	A	B
Low Atrazine	4	B	A	B	A	B	A	A	B
High Atrazine	4	C	C	A	B	A	A	A	A

Stellaria and Lamium cover initially decreased with increasing chemical treatment and did not change with time. Veronica cover was highest at the low treatment and lowest at the high treatment for the first two samplings; after that, the control and low treatment were not significantly different. Erodium had higher cover values with atrazine treatment initially but, by the fourth sampling, treatments were not significantly different.

The Calandrinia and Poa neighborhoods differed only slightly, with Stellaria and Poa cover patterns not changing. Veronica increased in cover at the low dose and decreased at the high for all four sampling periods, unlike Veronica in Poa neighborhoods. Lamium cover decreased with increasing treatment at the second and third sampling as it did in the Poa neighborhoods, but there was no significant difference between the control and the low treatment at the first and last sampling. Capsella cover differed between neighborhoods at sampling periods two and four, but the pattern remained the same. In Calandrinia neighborhoods, Erodium cover changed less in response to treatment than in Poa neighborhoods.

2,4-D - The 2,4-D control communities were dominated by Veronica for the first two sampling periods (Figure 3). By the end of the experiment, it had completed its life cycle and was dying, much as Lamium had done the year before. Calandrinia was the co-dominant with Veronica at the third sampling period and with Erodium by the fourth. Poa, Stellaria and Capsella remained minor species except for Capsella, which bolted, producing a flowering stalk penetrating the canopy by the fourth sampling period.

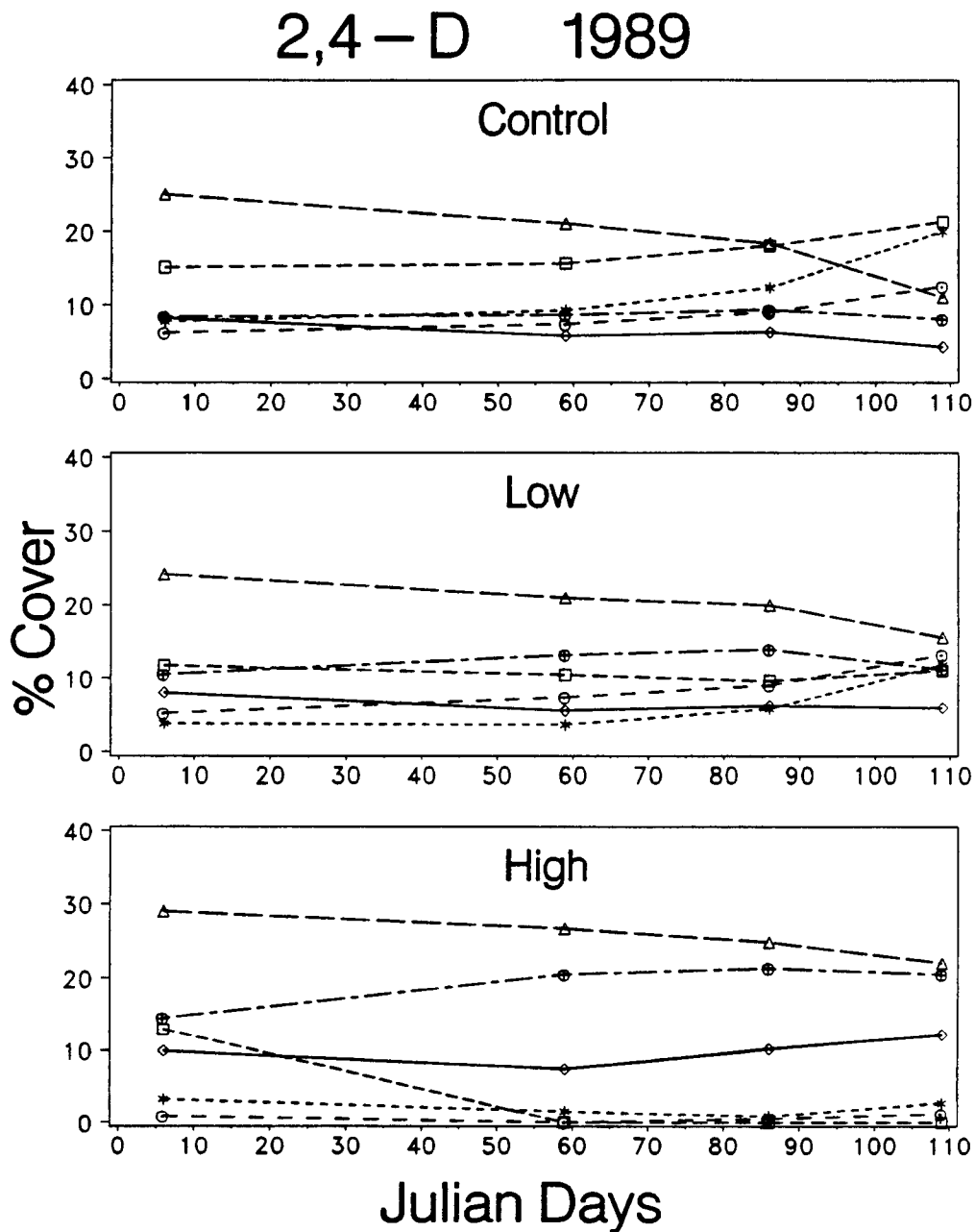


Figure 3. Percent cover over time of the six species with the highest cover values for the 1989 experiment using 2,4-D. The data are from 20 cm diameter neighborhoods. Each symbol is the mean of 30 samples, 10 from each of three replicate communities. Species: ◇ -STME △ -VEPE * -ERCI ⊕ -POAN and POBU □ -CACI ⊖ -CABU. Species codes are defined in Table 2. Julian days are from the beginning of the calendar year.

Calandrinia, Erodium and Capsella cover decreased in communities treated with low concentrations of 2,4-D (Figure 3). Erodium and Capsella started to make a recovery by the fourth sampling but Calandrinia did not.

The high treatment of 2,4-D caused major changes, virtually eliminating Capsella, Calandrinia, and Erodium (Figure 3). Calandrinia was unaffected until the second sampling period. Veronica cover slowly decreased with time, but maintained its dominance through all four samplings. Poa and Stellaria both increased cover under this treatment. Poa became a co-dominant with Veronica by the second sampling.

Poa neighborhoods treated with 2,4-D responded differently than when treated with atrazine (Table 5). 2,4-D did not decrease Stellaria cover and by the later samplings the high treatment had more Stellaria cover than the control. Initially, Veronica cover was significantly higher in the high treatment; by the third sampling all treatments were significantly different, with cover increasing with increasing chemical concentration. Poa cover increased with dosage as it did with atrazine treatments. However, by the fourth sampling there was no significant difference between the control and low treatment. Lamium cover was unaffected at the first and fourth sampling, but at the second and third sampling there was an increase in cover with higher chemical dose. Calandrinia cover values were similar at the first sampling, but by the third sampling cover decreased with dose, and all treatments were significantly different. Cover of Capsella decreased at the high concentration at all sample times, almost the reverse of its response to atrazine. Erodium cover decreased with chemical treatment; all treatments differed significantly by the third sampling.

By the second sampling, almost all individuals of Calandrinia in the high treatment of 2,4-D were killed and all Calandrinia targets were dead, so measurement of these neighborhoods was terminated (Table 5). The difference between the Poa and Calandrinia neighborhoods was slight. Comparison was difficult due to the loss of the high treatment. The impact of 2,4-D on Calandrinia showed up at the first sampling on the Calandrinia neighborhoods, whereas in Poa neighborhoods it did not become clear until the second or third sampling. Stellaria had higher cover values at the first sampling in the 2,4-D treatment in the Calandrinia neighborhood. This did not show up until the third sampling in the Poa neighborhood. Another difference was that Lamium had no response to 2,4-D treatment whereas in Poa neighborhoods at sampling periods two and three there was a treatment response.

Malathion - The same controls were used for both the 2,4-D and malathion treatments. The results from the control treatments are given in the 2,4-D section. There was little difference between the high and low malathion treatments (Figure 4), but there were subtle differences between the chemical treatments and the controls. Calandrinia did not become dominant or co-dominant until the fourth sampling, later than in the control. Erodium had a similar delayed increase. Poa cover increased slightly with malathion treatment. The other species showed no detectable changes.

Malathion had much less impact than did 2,4-D and atrazine (Table 6). Stellaria, Lamium and Capsella showed no treatment effect at any sampling period when in Poa neighborhoods. Malathion treatment decreased Erodium cover similarly at both the low and high treatments. This pattern did not change with

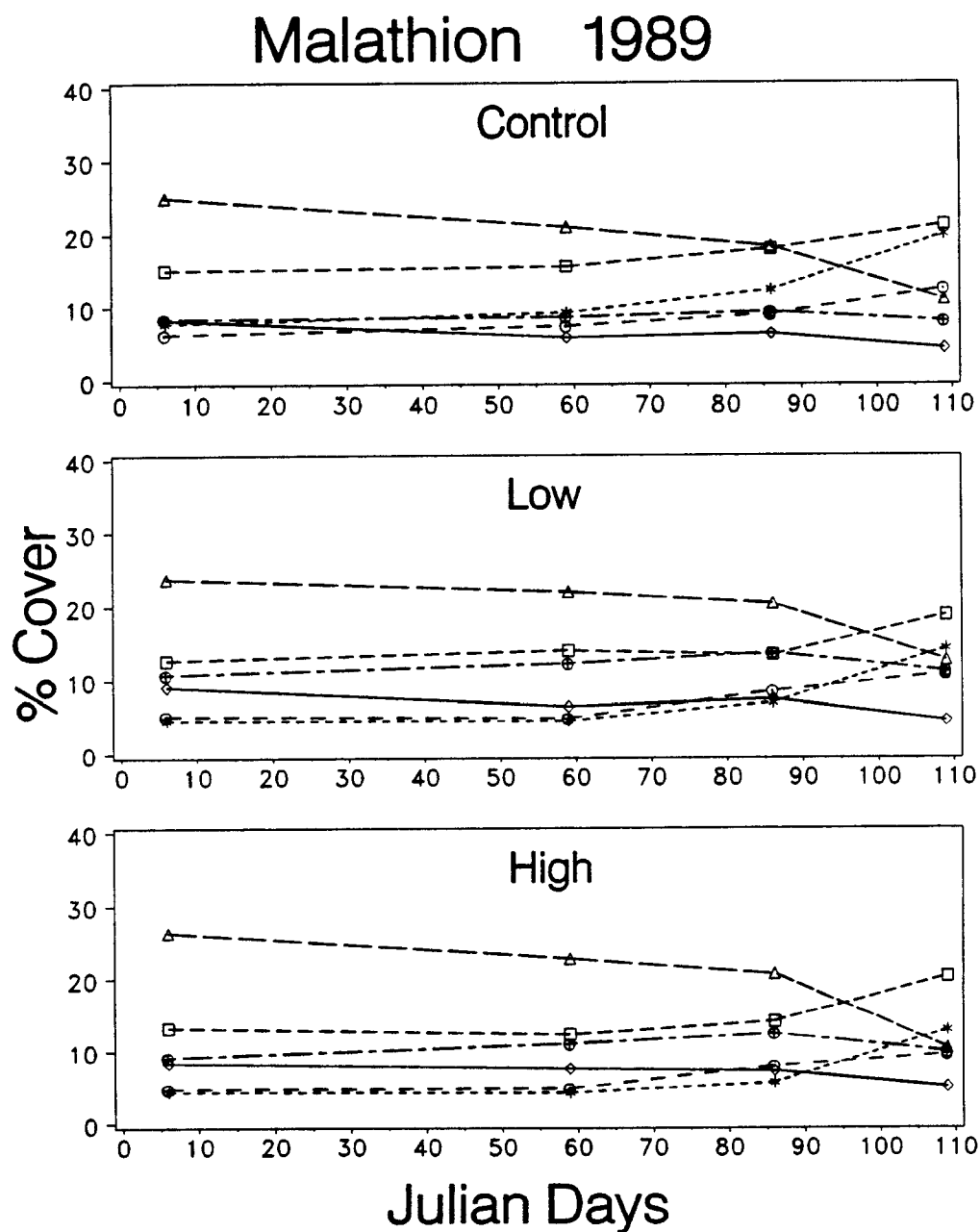


Figure 4. Percent cover over time of the six species with the highest cover values for the 1989 experiment using malathion. The data are from 20 cm diameter neighborhoods. Each symbol is the mean of 30 samples, 10 from each of three replicate communities. Species: ◇ -STME △ -VEPE * -ERCI + -POAN and POBU □ -CACI ○ -CABU. Species codes are defined in Table 2. Julian days are from the beginning of the calendar year.

Table 6. Significance of treatment differences for cover within species and sampling times, for malathion in 1989, using a protected LSD ($\alpha \leq .05$, $DF = 87$). The data are from 20 cm diameter neighborhoods around each of two target species. A = largest mean value, C = smallest mean value. Treatments with the same letter are not significantly different. Species codes are defined in Table 2.

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 20 cm									
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CACI	CABU	ERCI	BARE GROUND
Control	1	A	AB	B	A	A	A	A	A
Low Malathion	1	A	B	A	A	A	A	B	A
High Malathion	1	A	A	AB	A	A	A	B	A
Control	2	A	A	B	A	A	A	A	B
Low Malathion	2	A	A	A	A	A	A	B	AB
High Malathion	2	A	A	A	A	A	A	B	A
Control	3	A	B	B	A	A	A	A	A
Low Malathion	3	A	AB	A	A	B	A	B	A
High Malathion	3	A	A	A	A	B	A	B	A
Control	4	A	A	B	A	A	A	A	B
Low Malathion	4	A	A	A	A	A	A	B	A
High Malathion	4	A	A	AB	A	A	A	B	A

TARGET = <u>Calandrinia ciliata</u> NEIGHBORHOOD = 20 cm circle									
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CACI	CABU	ERCI	BARE GROUND
Control	1	A	A	B	A	A	A	A	B
Low Malathion	1	A	A	A	A	B	A	A	A
High Malathion	1	A	A	B	A	B	A	A	AB
Control	2	A	A	B	A	A	A	A	A
Low Malathion	2	A	A	A	A	A	A	A	A
High Malathion	2	A	A	AB	A	A	A	A	A
Control	3	A	A	B	A	A	A	A	B
Low Malathion	3	A	A	A	A	B	A	B	A
High Malathion	3	A	A	AB	A	B	A	B	A
Control	4	A	A	B	B	A	A	A	B
Low Malathion	4	A	A	A	B	A	A	B	A
High Malathion	4	A	A	AB	A	A	B	B	A

time. In contrast, cover of Poa increased similarly in both the low and high treatments. There was also an indication, even at the low concentration, that bare ground increased with treatment.

Again, with malathion, there were only a few differences between the Poa and Calandrinia neighborhoods. The most notable differences were 1) Veronica cover in Calandrinia neighborhoods was not significantly different among treatments; 2) the cover of Lamium was greater in the high treatment at the fourth sampling period; and 3) Erodium had no significant differences between treatments until the third sampling, a contrast to its response in the first sampling in the Poa neighborhoods.

TARGET BIOMASS

Means were calculated for target biomass for each species in each treatment. An ANOVA with a protected LSD multiple means test was used to determine if differences existed between treatments in target performance (Table 7). Both Poa and Calandrinia increased in biomass with increasing atrazine treatment in 1988. The atrazine treatment killed or decreased growth on several neighboring species in these communities while having a minimal negative effect on the target species (Figure 1). The application of 2,4-D had a similar positive response on Poa, although not as pronounced. In contrast, 2,4-D was toxic to Calandrinia and killed it at the high concentration. Malathion treatment had no significant impact on Poa biomass and the effect on Calandrinia was inconclusive (Table 7). In general, the target individuals reacted no differently (Table 7) than did the species as a whole

in the communities (Figure 1).

Table 7. The mean aboveground biomass (g) of target individuals (N = 30 for each treatment). ANOVA results using a protected LSD with log transformed biomass ($\alpha \leq .05$). A = largest mean treatment value, C = smallest mean treatment value for each species and chemical treatment. Treatments with the same letter within each experiment are not significantly different.

TARGET SPECIES	TREATMENT		
	CONTROL	LOW	HIGH
ATRAZINE			
<u>Poa</u>	0.064 C	0.316 B	0.447 A
<u>Calandrinia</u>	0.080 C	0.489 B	1.358 A
2,4-D			
<u>Poa</u>	0.043 B	0.032 B	0.058 A
<u>Calandrinia</u>	1.246 A	0.358 B	died
MALATHION			
<u>Poa</u>	0.043 A	0.042 A	0.038 A
<u>Calandrinia</u>	1.246 A	0.610 B	0.982 AB

INTERSPECIFIC COMPETITION

The presence of interspecific competition was determined by multiple regression analysis, using the percent cover or aboveground biomass of each species as the predictor variables for biomass of individual target plants. Cover and biomass were measured in both ten and twenty cm diameter neighborhoods around both target species, Poa and Calandrinia. Cover values were measured four times during each experiment (1988 and 1989). Aboveground biomass of target plants and their neighbors was measured at the conclusion of each sampling season.

Regression using cover values

1988, atrazine treatments, Poa targets - In the control treatment, Lamium was the only species in the 10 cm Poa neighborhoods that had interactions that were consistently significant (i.e., statistically significant in at least three of the four sampling periods) (Table 8). In contrast, however, Lamium was not a dominant species in the control neighborhoods, as measured by aboveground biomass (Figure 1), or a consistent competitor in the 20 cm neighborhoods (Table 8). All major species had a significant negative effect on target biomass at the second sampling period in the control treatment; this sampling was also the most important period of interspecific competition as measured by R^2 (Table 8). Some species in the control and low treatments had a unique response, in which signs of statistically significant interactions reversed in successive samplings (10 cm controls - LAPU and CACI; 10 cm low atrazine - CACI; and 20 cm low atrazine, LAPU)(Table 8). This did not occur in the other experiments.

Table 8. Regression coefficients from multiple regression (DF = 29) for atrazine in 1988. $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND	R ² %
Control	1	-0.37	0.36	-0.01	0.17	-0.33	-0.22	0.0	-0.93	25
Control	2	-1.29**	-0.87**	-0.01**	-1.02**	-0.58**	-0.96**	0.0	-0.51	50
Control	3	1.0	0.88	0.01*	0.94**	0.61	0.22	0.62	0.45	25
Control	4	-0.02	-0.06	-0.01**	0.11	0.01	-0.01	-0.01	0.74**	42
Low Atrazine	1	-0.83**	1.97	-0.06	-0.44	-0.63*	-0.58*	0.0	-0.48	28
Low Atrazine	2	-1.19**	-1.02*	-0.02**	-0.65*	-0.63	-1.34**	0.0	0.0	49
Low Atrazine	3	-0.89**	-0.21	-0.01**	0.66**	-0.51*	-0.64**	4.75**	0.0	70
Low Atrazine	4	-0.58**	-1.46**	0.004	-0.34	-0.51*	-0.54**	1.92**	0.0	69
High Atrazine	1	0.0	-0.74*	-0.02	-0.03	-0.40	-0.98**	-0.90	-0.53	30
High Atrazine	2	0.33	-0.59*	0.05	-0.12	-0.53	-0.68**	0.0	0.41	40
High Atrazine	3	1.12	-0.37	-0.01	0.17	-0.32	-0.64*	-0.03	-0.28	25
High Atrazine	4	0.48	-0.18	0.01	0.34	-0.06	-0.27	-0.10	-0.04	18

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND	R ² %
Control	1	-0.45	-0.30	-0.002	0.09	-0.55*	-0.64	-0.34	0.0	30
Control	2	-0.62	-0.26	-0.002	-0.04	-0.17	-0.24	-0.45	0.0	26
Control	3	0.68*	0.74**	0.01**	0.91**	0.45**	0.19	0.73**	0.34	44
Control	4	0.23	-0.26	-0.01	-0.41	0.02	-0.22	-0.12	-0.46	24
Low Atrazine	1	-0.02	-2.32**	0.02**	-0.12	0.05	-0.31	0.0	0.53	34
Low Atrazine	2	0.31	-0.25	-0.01**	0.50	0.18	-0.77	0.0	0.0	26
Low Atrazine	3	-1.18**	-0.58	-0.01**	-0.54	-0.35	-0.88**	2.66**	0.0	57
Low Atrazine	4	-0.22	-1.01*	0.01**	-0.07	-0.14	-0.18	1.55**	0.0	64
High Atrazine	1	1.16	-0.76	-0.20	0.19	-0.76	-1.09**	-0.16	-1.14*	41
High Atrazine	2	0.0	-0.68*	0.04	-0.43	-0.74	-0.46	0.0	-0.43	29
High Atrazine	3	0.21	-0.34	-0.01	0.50	-0.50	-0.68*	-0.21	-0.17	34
High Atrazine	4	-0.42	-0.71	0.02*	0.03	-0.21	-0.72*	-1.57	-0.48	24

With low atrazine treatment, Stellaria, Capsella, and Erodium were consistent competitors in the 10 cm neighborhoods, while Lamium was the only species consistently significant in the 20 cm neighborhoods. Veronica, the major biomass contributor to the low atrazine community (Figure 1), was not a consistent competitor. The low treatment had the highest level of interspecific competition (as measured by R^2) at the third and fourth sampling, later than in the control. The low treatment had more significant species interactions (19) than either the control (9) or the high (5) treatments, indicating a dispersion of interspecific competition amongst many species and over time (Table 8). This same pattern was found in the 20 cm neighborhoods, with the low treatment having the most significant species interactions (10) and the high treatment the least (5).

The high treatment had only Erodium as a consistent competitor, with the second sampling in the 10 cm neighborhood and the first sampling in the 20 cm neighborhood having the most interspecific competition (highest R^2). Erodium, while a consistent competitor in both the high and low treatments, was only a minor contributor to community biomass under all treatments (Figure 1).

1988, atrazine treatments, Calandrinia targets - In the control, the 10 cm neighborhoods had Capsella as the consistent competitor (Table 9). With atrazine treatment, Stellaria was the consistent competitor in the low treatments and Veronica in the high treatments. In contrast, the 20 cm neighborhoods had no consistent competitors in either the control or low treatments, but Veronica remained a consistent competitor in the high treatments. Whether a species was a consistent competitor in either 10 and 20 cm neighborhoods had no relationship to its contribution to the community biomass (Figure 1).

Table 9. Regression coefficients from multiple regression (DF = 29) for atrazine in 1988. $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TARGET = <i>Calandrinia ciliata</i> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.52**	-3.71*	-0.42	0.04	-0.42*	0.69*	-1.43**	0.0	44
Control	2	-0.48	-0.18	-0.15	-0.01*	-0.85**	0.05	-1.12	0.0	29
Control	3	-0.77	-0.48	-0.74	-0.01	-0.56**	-0.44	-1.31	0.0	20
Control	4	0.07	-0.17	0.30	0.01	0.17	0.15	0.0	0.0	22
Low Atrazine	1	-1.58**	-1.86	-1.34**	0.004	-0.43	-0.75	0.41	-0.87	53
Low Atrazine	2	-0.7	-0.91	-0.46	0.0002	-0.44	-1.14	-1.09	0.0	23
Low Atrazine	3	-0.96**	-0.99**	0.10	0.01	-0.09	-0.31	0.06	-1.24	39
Low Atrazine	4	-1.20**	0.01	-0.18	0.002	-1.09**	-0.77*	0.05	-1.40	46
High Atrazine	1	0.0	-1.95**	-0.42	-0.11	-0.93	-0.79	-0.79	-1.58*	20
High Atrazine	2	-0.7	-1.32**	-0.59	-0.07	-0.96	-0.77	0.0	-1.15**	27
High Atrazine	3	-1.95	-1.33**	-0.53	0.0	-1.94**	-1.52**	-1.58	-1.85**	54
High Atrazine	4	-0.86	-1.09**	-1.28**	0.09	-0.90*	-1.24**	-1.09	-1.61**	51
TARGET = <i>Calandrinia ciliata</i> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.74**	-0.52	-0.66	-0.001	-0.52**	0.39	-0.57	0.0	42
Control	2	0.20	-0.09	0.57	-0.002	0.16	0.10	-0.56	0.0	12
Control	3	-0.73*	-0.44	-0.14	-0.005	-0.10	-0.41	-0.38	-0.41	20
Control	4	-0.47	-0.36	-0.20	0.001	-0.13	0.16	0.0	0.0	27
Low Atrazine	1	-0.96	-1.65	-1.13	-0.002	-0.64	-0.98	-0.94	0.03	19
Low Atrazine	2	-1.56	-0.92	-0.89	0.01	-0.88	-0.88	-1.08	-3.49	22
Low Atrazine	3	-1.37**	-0.70	0.65	0.02	0.64	-1.21*	-0.97	-2.68	45
Low Atrazine	4	-0.90	-0.69	0.31	0.01	-0.29	-0.71	-0.70	3.48	38
High Atrazine	1	0.0	-3.53*	-0.81	-0.13	-1.62	-0.98	-0.52	-3.27**	31
High Atrazine	2	-0.09	-1.69**	-1.62	-0.04	-1.18	-0.87	0.0	-1.31	24
High Atrazine	3	2.63	-0.80	-1.47	0.0	-2.68**	-1.24*	-4.45**	-1.23*	40
High Atrazine	4	-0.49	-1.63**	-2.39**	0.01	-2.21**	-1.47**	-1.45	-2.12**	39

In both the 10 and 20 cm Calandrinia neighborhoods, the high treatment had the most interactions (Table 9). Control neighborhoods had the highest level of competition (R^2) at the first sampling, in contrast to the high treatment where the third and fourth sampling were highest. The importance of interspecific competition as measured by R^2 was greater in the low (53%) and high treatments (54%) than in the control (44%), while in the 20 cm neighborhoods there was little difference among treatments (Table 9). The number of significant competitive interactions in the 10 cm neighborhoods increased with time in the high treatment and occurred later than the control. A similar but less distinct pattern occurred in the 20 cm neighborhoods.

1988, atrazine treatment, target comparison - Both targets had more significant interactions in the 10 cm neighborhoods than in the 20 cm neighborhoods. Little new information was gained from the larger neighborhood, except that the area of influence was less than 20 cm when measured by cover. Therefore, the description that follows is limited to the 10 cm neighborhoods.

Atrazine treatment changed competitive scenarios and period of important competition for both target species. Poa and Calandrinia respond differently to chemical treatment and competition. Control treatments of Poa neighborhoods had Lamium as a consistent significant species and competition was most important (highest R^2) in the second sampling (Table 8), while in Calandrinia controls, competition was most important at the first sampling with Capsella as the consistent competitor (Table 9). In the low atrazine treatments, both targets had Stellaria as a significant competitor, while Poa targets also had Capsella and Erodium.

Competition was more important in the low treatments at the third and fourth sampling with Poa targets and the first and fourth sampling with Calandrinia targets. Erodium was a consistent competitor of Poa targets in the high treatments, while Veronica was with the Calandrinia targets. Competition in the high atrazine treatment was important earlier in the Poa neighborhoods than in Calandrinia neighborhoods. The number of significant interactions in the high treatment (5) was less than in the control (9) in the Poa neighborhoods, while they were similar (9 to 8) in the Calandrinia neighborhoods. The Poa neighborhoods had the most significant interactions in the low treatment, whereas in Calandrinia neighborhoods the high treatment had the most.

1989, 2,4-D and malathion treatments, Poa targets - Erodium was a consistent competitor in the 10 cm control neighborhoods (Table 10). In contrast, both 2,4-D treatments for Poa (Table 10) and the high malathion treatment (Table 11) had no consistent competitors in either the 10 or 20 cm neighborhoods. The 20 cm neighborhoods of the low malathion treatment had Calandrinia as a consistently important competitor and it was also the most productive species. In contrast, Calandrinia was the most productive species in the control communities (Figure 1), but it was only a significant competitor once in the control 10 or 20 cm neighborhoods. Other species (Veronica, Capsella, and Erodium) that were productive in the control community all were significant competitors in at least two samplings.

Table 10. Regression coefficients from multiple regression (DF = 29) for 2,4-D in 1989. $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2. The same control data were used in both tables 10 and 11.

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.15	-0.38*	0.05	-0.05	-0.10	-0.12	0.02	-0.21*	34
Control	2	-0.18*	-0.18	0.03	0.04	-0.13	-0.14*	-0.05	-0.20	34
Control	3	-0.02	-0.20	0.17	0.001	-0.15*	-0.11*	-0.05	-0.20**	45
Control	4	-0.09	-0.25**	0.0	-0.22*	-0.24**	-0.27**	-0.20**	-0.28**	48
Low 2-4,D	1	0.08*	0.14*	0.02	0.07	0.05	0.01	0.05	0.09	25
Low 2-4,D	2	0.11*	-0.04	-0.01	-0.003	-0.05	-0.03	-0.02	-0.06	29
Low 2-4,D	3	0.02	-0.001	0.03	0.01	-0.04	-0.04	-0.01	-0.07	30
Low 2-4,D	4	0.02	0.11	0.06	0.03	0.09*	0.06	0.03	0.13	23
High 2-4,D	1	-0.12	-0.12	-0.12	-0.06	0.02	-0.05	-0.20	-0.26	19
High 2-4,D	2	-0.07	-0.13	-0.07	0.0	0.0	-0.09	-0.06	-0.32**	21
High 2-4,D	3	-0.11	-0.32**	-0.11	0.0	-0.17	-0.07	-0.12*	-0.37**	37
High 2-4,D	4	0.15	-0.09	-0.41	0.0	-0.04	-0.01	-0.03	0.03	35

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.09	-0.07	0.03	0.06	-0.001	-0.08	-0.10	-0.07	14
Control	2	-0.02	-0.20	0.09	0.03	-0.13	-0.12	-0.05	-0.08	25
Control	3	-0.04	-0.37	0.02	-0.06	-0.19	-0.17*	-0.13	-0.19	26
Control	4	0.07	-0.57**	0.0	-0.40**	-0.43**	-0.40**	-0.13*	-0.21*	59
Low 2-4,D	1	0.11	0.25*	0.04	0.14*	0.11	0.05	0.14*	0.16	24
Low 2-4,D	2	0.14*	-0.05	-0.02	0.001	-0.04	-0.01	0.003	-0.01	27
Low 2-4,D	3	0.08	0.13	0.07	0.03	0.05	0.05	0.06	0.06	15
Low 2-4,D	4	0.06	0.18**	0.06	0.08	0.10*	0.09*	0.11**	0.16*	29
High 2-4,D	1	0.22	0.06	-0.08	0.02	-0.20	0.04	-0.04	0.01	25
High 2-4,D	2	-0.06	-0.26	-0.22	0.0	0.0	-0.08	-0.17	-0.47**	41
High 2-4,D	3	-0.10	-0.47**	-0.31**	0.0	-0.23	-0.15	-0.23**	-0.44**	46
High 2-4,D	4	0.09	-0.15	-0.50	0.0	-0.15	-0.03	-0.08	-0.11	33

Table 11. Regression coefficients from multiple regression (DF = 29) for malathion in 1989. $y = \beta_0 + \beta_1x_1 + \dots + \beta_9x_9$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2. The same control data were used for both tables 10 and 11.

TARGET = <u>Poa annua</u> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.15	-0.38*	0.05	-0.05	-0.10	-0.12	0.02	-0.21*	34
Control	2	-0.18*	-0.18	0.03	0.04	-0.13	-0.14*	-0.05	-0.20	34
Control	3	-0.02	-0.20	0.17	0.001	-0.15*	-0.11*	-0.05	-0.20**	45
Control	4	-0.09	-0.25**	0.0	-0.22*	-0.24**	-0.27**	-0.20**	-0.28**	48
Low Malathion	1	0.06	-0.07	-0.14	0.02	-0.05	-0.02	-0.13	-0.01	21
Low Malathion	2	0.02	0.002	-0.11	0.02	0.17	0.06	0.02	0.25	28
Low Malathion	3	-0.04	-0.15	-0.06	-0.07	-0.04	-0.06	-0.07	-0.002	14
Low Malathion	4	-0.02	-0.17	0.0	-0.23**	-0.03	-0.14*	-0.08	-0.06	45
High Malathion	1	-0.08	-0.07	-0.002	-0.05	-0.07	-0.06	-0.09	-0.10	25
High Malathion	2	0.01	0.01	-0.04	-0.03	-0.08*	-0.10**	-0.02	-0.11	40
High Malathion	3	0.001	0.07	0.08	0.02	0.02	0.02	0.002	0.01	23
High Malathion	4	-0.06	0.01	0.04	-0.03	-0.04	0.05	0.02	-0.04	34
TARGET = <u>Poa annua</u> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	LAPU	CACI	CABU	ERCI	RARE	BARE GROUND%	R ²
Control	1	-0.09	-0.07	0.03	0.06	-0.001	-0.08	-0.10	-0.07	14
Control	2	-0.02	-0.20	0.09	0.03	-0.13	-0.12	-0.05	-0.08	25
Control	3	-0.04	-0.37	0.02	-0.06	-0.19	-0.17*	-0.13	-0.19	26
Control	4	0.07	-0.57**	0.0	-0.40**	-0.43**	-0.40**	-0.13*	-0.21*	59
Low Malathion	1	0.26	-0.15	0.26	-0.04	-0.04	0.03	-0.14	0.13	30
Low Malathion	2	-0.17	-0.44*	-0.28	-0.43**	-0.19	-0.31**	-0.09	-0.39	35
Low Malathion	3	0.03	-0.26	0.32*	-0.19**	-0.23**	-0.11	-0.14	-0.14	49
Low Malathion	4	-0.08	-0.24**	0.0	-0.36**	-0.15*	-0.27**	-0.14*	-0.29	63
High Malathion	1	-0.04	-0.11	-0.10	-0.12*	-0.10**	-0.13**	-0.13**	-0.17**	43
High Malathion	2	0.06	0.18*	0.03	0.06	-0.02	0.06	0.11*	0.07	36
High Malathion	3	0.00	0.22*	0.01	0.05	0.01	0.05	0.01	0.10	19
High Malathion	4	-0.08*	0.08	0.02	0.02	-0.09*	-0.001	-0.01	-0.20**	43

When measured by the number of significant species interactions, interspecific competition was more common in the 10 cm neighborhood controls (10) than in either treatment for 2,4-D (4, 2) and malathion (2, 2) . In contrast, in the 20 cm neighborhoods for the low treatments, competitors were more diverse (Tables 10, 11). The importance of interspecific competition (R^2) increased with time in both the 10 and 20 cm control neighborhoods and in the 20 cm neighborhoods in the low malathion treatment. The importance of competition decreased in 10 cm neighborhoods with 2,4-D and malathion treatment, when measured either by the number of significant species interactions or by the highest R^2 per treatment (Tables 10, 11). A similar pattern was present in 20 cm neighborhoods for 2,4-D but not for malathion. With both chemicals, Erodium became a less important competitor (Tables 10, 11) as its biomass decreased with treatment (Figure 1).

1989, 2,4-D and malathion treatments, Calandrinia targets - Ten and 20 cm control neighborhoods of Calandrinia targets had Poa and Erodium as consistent competitors, with Capsella also consistent in the 10 cm neighborhoods (Table 12). All three were productive in the control communities (Figure 1). Only Erodium was a consistent competitor in the 10 cm neighborhoods of the low 2,4-D treatments. High levels of 2,4-D killed the target plants. Malathion treatments had no consistent competitors (Table 13).

The importance of competition, as measured by the highest R^2 per treatment, decreased with 2,4-D treatment. In contrast, competition was the most important in the high treatment for malathion. The number of significant interactions decreased with increasing chemical treatment and with increased neighborhood

Table 12. Regression coefficients from multiple regression (DF = 29) for 2,4-D in 1989. $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2. The same control data were used for both tables 12 and 13.

TARGET = <u>Calandrinia ciliata</u> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CABU	ERCI	RARE	BARE GROUND %	R ²
Control	1	-0.64	-2.86	-9.78**	-1.90	-2.63	-2.84	-4.13	0.03	38
Control	2	-1.38	-5.79**	-8.32**	-0.61	-2.77**	-1.79**	-2.38	-2.97	75
Control	3	-1.37	-6.90**	-4.97**	-2.12	-4.63**	-3.27**	-3.20	-5.07**	67
Control	4	-0.79	1.78	-7.13**	0.0	-3.41**	-2.34**	-2.68**	-4.32*	59
Low 2-4,D	1	-0.13	-1.64	-0.79	-1.47	-2.85**	-2.37**	-3.87**	-2.39*	47
Low 2-4,D	2	0.46	0.04	-1.56	-2.11	-0.95	-2.01**	-2.23*	-2.95	43
Low 2-4,D	3	-2.65*	-2.08	-3.14**	-0.98	-1.63*	-1.86**	-2.64**	-2.83*	58
Low 2-4,D	4	0.08	0.85	-2.65	0.0	0.17	-0.38	-1.63	-0.33	33
High 2-4,D		TARGET KILLED								

TARGET = <u>Calandrinia ciliata</u> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CABU	ERCI	RARE	BARE GROUND %	R ²
Control	1	2.15	-7.81*	-9.08*	-0.76	-2.39	-2.55	2.63	-0.22	44
Control	2	1.22	-8.47**	-7.25**	0.65	-2.63	-2.59*	-0.85	-2.4	57
Control	3	-6.19**	-3.34	-9.99**	-2.25	-2.99	-4.18**	-2.14	-4.50	54
Control	4	0.61	-3.60	-7.18**	0.0	-4.57**	-6.95**	-3.77*	-5.86	53
Low 2-4,D	1	0.48	0.17	0.40	1.64	0.34	-0.39	-1.36	-0.19	22
Low 2-4,D	2	-1.34	5.02*	1.52	2.26	-0.22	-0.28	-1.37	-0.01	39
Low 2-4,D	3	-0.10	1.77	-2.48	-2.20	-0.10	-0.50	-0.76	1.07	33
Low 2-4,D	4	1.71	-0.19	-4.17*	-0.58	0.49	-0.61	-1.35	1.60	39
High 2-4,D		TARGET KILLED								

Table 13. Regression coefficients from multiple regression (DF = 29) for malathion in 1989. $y = \beta_0 + \beta_1x_1 + \dots + \beta_9x_9$; where y = target biomass, β = coefficients fitted for the regression, x_1 = cover of STME, x_2 = cover of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2. The same control data were used for both tables 12 and 13.

TARGET = <i>Calandrinia ciliata</i> NEIGHBORHOOD = 10 cm circle										
TREATMENT	TIME	STME	VEPE	POAN POBU	LAPU	CABU	ERCI	RARE	BARE GROUND %	R ²
Control	1	-0.64	-2.86	-9.78**	-1.90	-2.63	-2.84	-4.13	0.03	38
Control	2	-1.38	-5.79**	-8.32**	-0.61	-2.77**	-1.79**	-2.38	-2.97	75
Control	3	-1.37	-6.90**	-4.97**	-2.12	-4.63**	-3.27**	-3.20	-5.07**	67
Control	4	-0.79	1.78	-7.13**	0.0	-3.41**	-2.34**	-2.68**	-4.32*	59
Low Malathion	1	-1.90	-3.91	2.24	-6.32**	-0.74	-3.66*	-1.07	-2.52	44
Low Malathion	2	-4.56**	-4.05**	-4.40**	-3.49**	-4.17**	-1.75	-1.27	-4.72**	58
Low Malathion	3	-1.76	-3.66**	-4.76**	-1.82	-4.39**	-1.50	-1.84	-3.51*	52
Low Malathion	4	-0.06	-0.66	-1.46	0.0	0.80	-0.72	-0.84	-3.20	22
High Malathion	1	-1.18	-10.08**	-0.92	-2.85	-1.75	-4.28	-2.49	-2.30	35
High Malathion	2	-0.83	-4.21	-5.83	-4.04	-2.30	-2.18	-2.12	-1.14	36
High Malathion	3	-4.39*	-3.23	-5.68**	-2.67	-1.83	-3.01**	-3.16*	3.10*	65
High Malathion	4	-0.71	1.18	-11.3**	-3.91	-2.45*	-2.35**	-4.04**	-4.33	68

TARGET = <i>Calandrinia ciliata</i> NEIGHBORHOOD = 20 cm circle										
TREATMENT	TIME	STME	VEPE	POAB POBU	LAPU	CABU	ERCI	RARE	BARE GROUND %	R ²
Control	1	2.15	-7.81*	-9.08*	-0.76	-2.39	-2.55	2.63	-0.22	44
Control	2	1.22	-8.47**	-7.25**	0.65	-2.63	-2.59*	-0.85	-2.4	57
Control	3	-6.19**	-3.34	-9.99**	-2.25	-2.99	-4.18**	-2.14	-4.50	54
Control	4	0.61	-3.60	-7.18**	0.0	-4.57**	-6.95**	-3.77*	-5.86	53
Low Malathion	1	-3.67	-0.15	-4.62	-6.8*	0.76	-2.98	0.21	-3.0	34
Low Malathion	2	-2.48	-3.06	-0.21	-5.97*	-0.08	-2.82*	-3.28*	-8.68**	40
Low Malathion	3	-4.62**	-8.26**	-6.25**	4.10	-1.65	-1.48	-4.41**	-3.52	36
Low Malathion	4	-1.43	-1.04	-0.11	0.0	-1.16	-1.56	-1.92	-9.4**	31
High Malathion	1	-11.81**	-6.30	-0.65	-1.48	-4.13	-3.64	-3.43	-5.36	22
High Malathion	2	-5.17	0.06	1.40	-2.35	-0.25	-2.41	-2.01	-5.41	12
High Malathion	3	-7.53	-7.48*	-1.87	-5.44*	-2.65	-4.31**	-4.02	-6.85*	44
High Malathion	4	-1.19	-0.08	-9.98**	-2.56	-2.90*	-3.02**	-4.26**	-7.00**	69

diameter. In both the 10 and 20 cm neighborhoods for the high malathion treatment, interspecific competition increased with time and was most important (largest R^2) in the fourth sampling. In contrast, interspecific competition was most important (R^2) at the second sampling and decreased thereafter in the control and low malathion treatments (Table 13).

Target comparison, 1989, 2,4-D and malathion treatments -Both targets had Erodium as a consistent competitor in all control neighborhoods, except in the Poa 20 cm neighborhoods, where it was significant twice (Tables 10, 12). In addition, the 10 cm neighborhoods of Calandrinia also had Capsella and Poa as consistent competitors (Table 12).

Chemical treatment changed or eliminated consistent competitors. With 2,4-D treatments, there were no consistent competitors in the low treatments for 2,4-D 10 cm Poa neighborhoods. In contrast, Calandrinia neighborhoods had Erodium and rare species as significant competitors (Tables 10, 11, 12, 13). The 20 cm neighborhoods of Poa targets in the low malathion treatment had Calandrinia as the consistent competitor. No other 20 cm neighborhood had significant competitors.

The number and timing of significant competitive interactions changed with target species and treatment. In the 20 cm neighborhoods with Poa targets, the low chemical treatment had the largest number of significant interactions, while with Calandrinia neighborhoods the control treatment had the highest number of significant interactions (Tables 10, 11, 12, 13). In the Poa neighborhoods with 2,4-D treatment, competition was most important in the third sampling period in three

of the four treatments (Table 10). In contrast, in the malathion treatments the most important period of competition differed from the control only in one of four treatments (Table 11). In contrast Calandrinia neighborhoods treated with high malathion had the most competition (highest R^2) at the fourth sampling versus the second in the controls (Table 13).

Competition was most important later in control Poa neighborhoods than in Calandrinia neighborhoods. However, competition was more important in Calandrinia neighborhoods, as measured by the highest R^2 per treatment, than in Poa neighborhoods (7 out of 10 comparisons) (Tables 10, 11, 12, 13). This contrasts with the 1988 atrazine experiment where Poa was most affected by competitors (5 out of 6 comparisons).

Differences between target species - Poa was a consistent competitor of Calandrinia in 10 and 20 cm 1989 control neighborhoods, but its importance decreased in neighborhoods treated with either malathion or 2,4-D, even though its biomass did not. Calandrinia consistently competed with Poa only in the 20 cm neighborhoods of the low malathion treatments, suggesting that Poa was generally the more competitive of the two species. In contrast, neither target species was a consistent competitor in the 1988 atrazine experiment.

Regression using aboveground biomass

In these regressions, biomass and maximum flower height of either target species, Poa or Calandrinia, were used as response variables and aboveground biomass of each species within either the 10 or 20 cm neighborhood was the predictor variable. Log transformations were used on the neighborhood biomass

data and an inverse transformation was used on the target biomass. No neighborhood biomass data were collected from the control communities in 1988 due to the entanglement of the aboveground plant parts, caused in part by the luxuriant growth of Stellaria. Measurements were taken at the conclusion of each experiment.

1988, atrazine treatments - The importance of competition (R^2) decreased with increased atrazine treatment in three out of four treatments when target biomass was the response variable (Table 14). In the 10 cm neighborhoods of the low atrazine treatment, Stellaria was significant and positive with either target. However, for the high treatment, where it was almost absent from the communities (Figure 1), Stellaria was not significant (Table 14). In Calandrinia neighborhoods, Veronica was a significant competitor in 10 cm neighborhoods with low atrazine and in the 20 cm neighborhoods with high atrazine treatment (Table 14). This occurred even though Veronica was no longer a dominant species in the high treatment communities (Figure 1).

Unexpectedly, Poa targets experienced intraspecific competition in only the 20 cm low treatment, even though there was a substantial increase in the community biomass of Poa from the low to the high treatments (Figure 1). Calandrinia targets also had a single intraspecific interaction, in the 20 cm high treatment.

When flower height instead of biomass was used as the response variable in atrazine treatments (Table 15), there were fewer significant species interactions (9 versus 13 with biomass); and five of the nine significant interactions were in the 20 cm high atrazine Poa neighborhoods. While using biomass as the response variable

Table 14. Regression coefficients from multiple regression (y = target biomass; x_1 = neighbor biomass) for atrazine in 1988 (DF = 20). $y = \beta_0 + \beta_1 x_1 + \dots + \beta_n x_n$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TREATMENT	TIME	STME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 10					R ² %
			VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	No Data										
Low Atrazine	4	.25**	-.08	-.05	.14	-.02	.24**	.002	-.10	-9.2*	48	
High Atrazine	4	-2.07	.15	.05	.37	.03	-.01	.16	.08	2.94	33	

TREATMENT	TIME	STME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 20					R ² %
			VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	No Data										
Low Atrazine	4	.09	.15	-.18**	-.08	.06	-.07	.06	-.10	-.29**	50	
High Atrazine	4	-.01	.11*	-.12	-.43**	.03	.19*	.07	.03	-.21	41	

TREATMENT	TIME	STME	TARGET= <u>Calandrinia ciliata</u>				NEIGHBORHOOD = 10					R ² %
			VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	No Data										
Low Atrazine	4	.26*	-.40**	.08	.11	-.21	.12	.02	-.38	2.48	59	
High Atrazine	4	.47	-.19	-.15	-2.10	.02	.04	-.03	.14	-.36	26	

TREATMENT	TIME	STME	TARGET= <u>Calandrinia ciliata</u>				NEIGHBORHOOD = 20					R ² %
			VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	No Data										
Low Atrazine	4	-.002	-.09	-.08	.15	-.04	.23**	.11	-.33	.07	28	
High Atrazine	4	.30	-.19**	-.05	-.14	.18**	.16	.11	-.02	-.34	38	

Table 15. Regression coefficients from multiple regression (y = target flower height; x_1 = neighbor biomass) for atrazine in 1988 (DF = 20). $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TARGET= <u>Poa annua</u> NEIGHBORHOOD = 10											
TREATMENT	TIME	STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	R ² %
Control	4	No Data									
Low Atrazine	4	-19.04	1.56	-5.77	-15.17	21.48	14.54	10.79	-48.98	-54.44	34
High Atrazine	4	22.23	-7.5	2.15	-29.11	-.44	10.31	-2.75	-7.14	-70.94	44
TARGET= <u>Poa annua</u> NEIGHBORHOOD = 20											
TREATMENT	TIME	STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	R ² %
Control	4	No Data									
Low Atrazine	4	-8.56	-14.61	9.41	6.41	-3.48	15.48**	1.69	-6.97	5.51	40
High Atrazine	4	-3.78	-5.28**	7.52**	18.7**	-4.21*	-4.7	-4.61*	1.0	12.52	53
TARGET= <u>Calandrinia ciliata</u> NEIGHBORHOOD = 10											
TREATMENT	TIME	STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	R ² %
Control	4	No Data									
Low Atrazine	4	-6.05	8.08	-2.9	-12.68	3.37	-6.85	-.61	22.16	-100.68	29
High Atrazine	4	2.37	-1.75	5.91	40.52	-1.44	-1.59	-.49	4.3	20.61	22
TARGET= <u>Calandrinia ciliata</u> NEIGHBORHOOD = 20											
TREATMENT	TIME	STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	R ² %
Control	4	No Data									
Low Atrazine	4	12.5	-6.4	8.05	-19.63**	1.69	-4.0	-4.05	6.6	-2.28	35
High Atrazine	4	-.72	4.38	-1.02	12.77	-6.20**	-.45	-10.06**	3.35	15.26	41

revealed more significant interactions, neither response variable was consistently better at measuring the importance of competition (R^2 values, Tables 14, 15).

1989, 2,4-D and malathion treatments, Poa targets - Ten cm neighborhoods with Poa targets had only two significant species interactions and both occurred in the high treatment (Table 16). In contrast, when flower height was the response variable there were no significant interactions in the high 2,4-D treatment while five appeared in the high malathion treatment (Table 17).

Poa targets had significant intraspecific competition in both the 10 and 20 cm high 2,4-D treatments (Table 16). This corresponds to the increase in Poa biomass in that treatment, while there was no significant difference between Poa biomass in the control and low atrazine treatments (Figure 1).

There were no significant interactions in the controls in either neighborhood size (Table 16). In contrast, when cover was the predictor variable, the controls had a number of significant interactions, especially at the fourth sampling just prior to biomass harvest (Table 10). The 10 and 20 cm neighborhoods of Poa targets had a similar pattern, with more significant species interactions with increased treatment (Table 16). This occurred when either biomass or flower height was the response variable (Tables 16, 17). When cover was the predictor, the high treatment generally had fewer significant interactions than the other treatments (Tables 10, 11).

Table 16. Regression coefficients from multiple regression (y = target biomass; x_1 = neighbor biomass) for 2,4-D and malathion in 1989 (DF = 17). $y = \beta_0 + \beta_1 x_1 \dots \beta_8 x_8$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TREATMENT	TIME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 10					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	
Control	4	-.03	-.02	-.14	.52	-.04	-.03	.02	.14	.04	54
Low 2-4,D	4	.2	-.08	.13	-.0001	-.04	.03	.06	.08	.01	22
High 2-4,D	4	-.03	-.004	-.14*	-.22	0.00	-.14	-.02	-.03	.07	35
Low Malathion	4	-.23	.09	-.08	.62	-.03	.09	.02	-.07	.07	49
High Malathion	4	.16**	.004	-.06	-.38	.01	-.01	.01	.03	.02	60

TREATMENT	TIME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 20					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	
Control	4	.04	.05	-.15	.22	-.005	.003	.006	.04	.04	39
Low 2-4,D	4	-.03	.003	.01	.02	.01	-.003	-.02*	-.01	-.01	73
High 2-4,D	4	-.04	.11*	-.13**	-.03	0.00	.05	-.02	.05*	.01	66
Low Malathion	4	.1	-.004	-.02	-.39**	.02	-.02	.02	-.04	-.04	84
High Malathion	4	.12*	-.02	-.02	-.19	.03	-.01	-.04**	-.03	.004	59

Table 17. Regression coefficients from multiple regression (y = target flower height; x_1 = neighbor biomass) for 2,4-D and malathion in 1989 (DF = 17). $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TREATMENT	TIME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 10					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	
Control	4	4.75	5.31	18.13**	-48.39	3.3	1.99	-1.13	-6.74	-2.51	55
Low 2-4,D	4	-38.77	20.72	-29.44	-.97	10.9	.13	-11.87	-15.94	.75	48
High 2-4,D	4	-5.44	.63	14.79	-3.71	0.0	90.32	-2.88	1.14	-12.18	35
Low Malathion	4	7.56	1.03	14.4	-27.07	2.94	-1.42	-1.77	16.36	-8.2	56
High Malathion	4	-38.9**	-10.86	15.78**	138.12**	-5.48*	-10.48**	.47	-1.29	-9.00	81

TREATMENT	TIME	TARGET= <u>Poa annua</u>				NEIGHBORHOOD = 20					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE	
Control	4	-2.25	-3.81	13.04	-37.48	-2.52	2.07	-.52	-5.07	-4.66	36
Low 2-4,D	4	7.48*	3.14	-3.55	-5.70	-.86	3.38	2.08	-.42	2.25	72
High 2-4,D	4	1.32	-4.36	10.96**	-29.05**	0.0	-10.65*	-4.28*	-.57	-3.12**	75
Low Malathion	4	-8.5	1.91	.43	18.96	-.4	3.21	-.57	7.54	2.46	33
High Malathion	4	-21.33	3.24	1.65	43.14*	-2.13	4.39	8.09**	2.88	.64	68

1989, 2,4-D and malathion treatments, Calandrinia targets - The 10 cm neighborhoods with Calandrinia targets had no significant interactions under any treatment using either biomass or flower height as the response variable (Tables 18, 19). In contrast, when cover was used as the predictor variable there were a number of significant interactions (Tables 12, 13), although none occurred during the fourth sampling in either low treatment, just prior to biomass harvest. The 20 cm neighborhoods had three significant interactions that were in either the control or low 2,4-D treatment when either biomass or flower height were used as the response variable (Tables 18, 19). In contrast, 2,4-D treatments using cover as the predictor variable had fewer significant interactions in the 20 cm neighborhoods than in the 10 cm neighborhoods (Table 12).

Table 18. Regression coefficients from multiple regression (y = target biomass; x_1 = neighbor biomass) for 2,4-D and malathion in 1989 (DF = 17). $y = \beta_0 + \beta_1 x_1 \dots \beta_8 x_8$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TREATMENT	TIME	TARGET= <u>Calandrinia ciliata</u> NEIGHBORHOOD = 10								R ² %	
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU		
Control	4	-.02	-.03	-.77	1.14	.1	.14	-.04	.5	.67	46
Low 2-4,D	4	-.24	-.4	-.22	.68	.43	-.1	-.08	-.79	-.2	58
High 2-4,D	4	Target Died									
Low Malathion	4	.24	-.08	.78	-.74	-.27	-.33	-.44	.26	.22	41
High Malathion	4	.32	-.15	-.12	-1.1	.14	.1	.34	-.07	.2	15

TREATMENT	TIME	TARGET= <u>Calandrinia ciliata</u> NEIGHBORHOOD = 20								R ² %	
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU		
Control	4	-.62**	-.22	.41	-.41	.1	.21*	-.01	.12	.06	64
Low 2-4,D	4	.15	-.05	-.57	.44	.24*	-.05	.07	.4	.04	49
High 2-4,D	4	Target Died									
Low Malathion	4	.09	-.25	-.09	-1.44	.05	-.14	-.04	.22	-.001	42
High Malathion	4	.13	.09	-.97	.79	.14	-.31	.02	.09	.16	49

Table 19. Regression coefficients from multiple regression (y = target flower height; x_1 = neighbor biomass) for 2,4-D and malathion in 1989 (DF = 17). $y = \beta_0 + \beta_1 x_1 + \dots + \beta_8 x_8$; where β = coefficients fitted for the regression, x_1 = biomass of STME, x_2 = biomass of VEPE, etc. * = significant at .1 level. ** = significant at .05 level. Species codes are defined in Table 2.

TREATMENT	TIME	TARGET= <u>Calandrinia ciliata</u>					NEIGHBORHOOD = 10					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	3.45	4.92	14.87	-22.19	-7.01	-2.45	-2.35	16.09	-25.50	36	
Low 2-4,D	4	12.83	28.81	17.69	38.17	-18.05	-1.41	2.77	58.15	-603.62	60	
High 2-4,D	4	Targets Died										
Low Malathion	4	-4.72	3.0	-26.02	32.82	9.0	10.68	11.22	-1.26	-6.58	37	
High Malathion	4	-17.91	4.48	7.15	71.5	1.28	-7.44	-13.76	4.49	-5.67	18	

TREATMENT	TIME	TARGET= <u>Calandrinia ciliata</u>					NEIGHBORHOOD = 20					R ² %
		STME	VEPE	POAN	LAPU	CACI	CABU	ERCI	POBU	RARE		
Control	4	19.7*	8.19	-13.24	26.98	-5.36	-5.96	-2.07	-7.19	-2.91	48	
Low 2-4,D	4	-13.21	16.63	23.26	-44.59*	-12.23*	3.35	-5.10	-17.97	-.51	59	
High 2-4,D	4	Targets Died										
Low Malathion	4	-5.94	8.56	7.08	24.07	-2.05	3.88	.24	-1.16	1.92	32	
High Malathion	4	-1.27	-8.6	37.21	-25.57	-4.26	6.74	-1.13	-4.56	-7.39	35	

DISCUSSION

BIOLOGY

This section discusses the biological interactions in terms of the effects on interspecific competition, the importance of competition and the use of biomass as a measure of competition. In addition, questions concerning the changes in biomass and species selectivity resulting from chemical application are addressed, followed by a section comparing these results with other types of removal experiments. Finally, the differences found between the fertilized (1988) and unfertilized (1989) controls are considered.

Competition is just one of many species interactions within plant communities. Other interactions such as allelopathy and herbivory cannot be discounted even though no evidence was found of either. In any community, numerous interactions are likely to be occurring, both positive and negative, with direct and indirect effects. This experiment was designed to enhance the probability of competition occurring. Synchronous seed germination was encouraged so dominance and suppression resulting from early emergence were diminished. Soil fertility was amended to ensure that resources were available for sufficient plant growth to insure interactions. Density dependent mortality occurred, which is generally considered a symptom of competition. The area where the experiments were conducted was isolated from major herbivores. The raised beds further isolated the experiments from the effects of the local soil conditions, including microsite variations. This circumstantial evidence does not prove that competition was the driving force structuring these communities. It is difficult to demonstrate conclusively that competition is the

process determining species dominance even in experiments with only two individuals, let alone in a complex community such as used here. However, the conditions and outcomes of the study strongly suggest that competition was a major contributor to the structure of these communities. Therefore, the experiments will be discussed in terms of competition.

Other processes besides interactions were probably altered by chemical treatments. Organic pollutants have the potential to alter community composition either directly through phytotoxicity or indirectly via secondary effects. The secondary effects of these chemicals can include increased nutrient uptake, resulting in increased herbivory and disease (see literature review). While not a factor in these experiments, temporary pollen sterility, decreased seed germination rates and slowed decomposition rates can also be produced by these pesticides, which would have an effect in natural environments.

Competition - Few studies have looked at the effects of organic pollutants on plant competition. In this study, interspecific competition was severely altered following application of organic compounds. The importance of interspecific competition increased in some situations (low atrazine treatments, Poa targets, Table 8) while it decreased in others (2,4-D treatments, Poa targets, Table 10). The onset of competition was delayed in Calandrinia neighborhoods treated with atrazine (Table 9), but not in other treatments. A major change following treatment was in the identity of influential competitors. The addition of a pollutant, even malathion, an insecticide developed for use on plants, changed the competitive hierarchy (as measured by the identity of consistent competitors) in almost every scenario tested

(Tables 8-13).

These results suggest that plant communities are being subtly altered by exposure to organic pollutants. Other studies investigating the relation between competition and anthropogenic stresses have found similar modifications. Changes occurred in the competitive balance in favor of ryegrass when grown with clover in a replacement series experiment exposed to ozone (Bennett and Runeckles, 1977). Bennett and Runeckles (1977) suggest that the clover was more sensitive to ozone and therefore grew less. The competitive balance within competing species pairs exposed to UV-B radiation often changed dramatically (Fox and Caldwell, 1978).

The results of competition are often measured in terms of some physical parameter of ecological significance, generally a substitute for fecundity, while the competitor is described by some other parameter such as biomass. In this study, aboveground biomass and flower height of the target species were measures of target success, while neighbor biomass or cover indicated the size of the competitor. Using different measures of success and of competitor size changed the pattern of apparent competition; little correlation was found between results using the different combinations of descriptors of target and competitor size.

The results of competition were discussed in terms of R^2 and number of significant competitors using regression analyses, but other components of the regression could have also been used. The size of the coefficient is an indication of the impact a particular species had on the target individuals. The sign of the coefficient indicates whether that species had a negative or positive impact on the target. In this study, a negative coefficient was interpreted to represent competition.

Eighty-eight percent of 297 statistically significant interactions were negative (Tables 8-13). However, in the atrazine experiments with Poa targets the regression coefficients were significant with both negative and positive signs (LAPU and CABU, Table 8). Morphological changes in Lamium and Calandrinia may provide a possible explanation for these changes. Lamium completed its life cycle before the other species. During the later samplings, its occupation of space may have represented a physical barrier to other species but not a biological sequestering of resources. Calandrinia, with its basal rosette type morphology, may also be occupying space. With both species the occupied space could otherwise have been filled with more competitive species such as Capsella and Erodium. The following year, the treatments were not fertilized and different patterns were present (Table 10).

Biomass and competition - Is aboveground biomass of the individual species within a community a good indicator of the species' competitive influence? Competitiveness is not solely related to biomass but incorporates other characteristics of a plant, including its architecture. These data do not support any consistent generalization about a relation between biomass and competitiveness. Four different patterns were found between species having either high (three species with highest biomass, Figure 1) or low (three species with the lowest biomass) biomass and competition. In the first pattern, significant competitive species at the fourth sampling had high biomass. This occurred in Calandrinia neighborhoods treated with 2,4-D (Table 12) and in the Poa neighborhoods treated with malathion, where the significant competitive species, Veronica, Calandrinia, Capsella, and

Erodium, had the most biomass. Also, in the Poa neighborhoods of the 1989 control communities, Erodium was the only consistent competitor (Table 10) and it was a dominant species in biomass (Figure 1). This pattern was present ten percent of the time. A second pattern, in which a species with high biomass was not a significant competitor, occurred 24 percent of the time. This pattern was exemplified by Stellaria in the 1988 control (Tables 8, 9). In contrast, Stellaria in the low atrazine treatment had low biomass and was a consistent competitor. This third pattern was also shown in Poa neighborhoods in the atrazine experiment where the major competitors (Lamium, Capsella, and Erodium) (Table 8) had low biomass (Figure 1). This pattern was the rarest, occurring only four percent of the time. The fourth pattern was exemplified by Lamium, which had low biomass and was not a significant competitor in these experiments. In fact, in Poa neighborhoods in the malathion experiment, Stellaria and Lamium had the least biomass and were not competitive in 21 out of 24 possible interactions (Table 11). This pattern occurred 30 percent of the time. The remaining significant interactions occurring at the fourth sampling period were with species having neither high or low biomass (33 percent).

Interestingly, species with similar basal rosette morphology, Capsella and Erodium, were important competitors regardless of their biomass contribution to the community. When they were reduced by chemical treatment (2,4-D), no other species replaced them as competitors.

The importance of interspecific competition - The importance of competition, as defined by Weldon and Slauson (1986), is the relative degree to which competition contributes to the overall decrease in growth rate, metabolism, fecundity,

or fitness of an organism below its optimal condition. They further defined the coefficient of determination in a size-distance regression analysis as a measure of the importance of competition, with the residual variation being attributed to such effects as environmental heterogeneity, herbivory, predation, genetic differences, disturbance, measurement error, and chance. In this experiment, precautions were taken to reduce or eliminate many of these sources of variation, and the relative importance of competition has probably been enhanced. Even under these 'ideal' conditions, the role of interspecific competition ranged from non-significance to accounting for up to 70 percent of the variation in target weight, when cover was used as the measure of neighbor size (Tables 8-13). The importance of interspecific competition in structuring natural communities has been questioned (Connor and Simberloff, 1979; Connell, 1983), but competition was influential in modifying these experimental communities.

The addition of a chemical stress to a community altered the timing of competition and the species that had the most competitive influence and, therefore, the importance of competition. Others have found that changes in nutrient level (Tilman, 1987; Carson and Pickett, 1990) and different physical environments change the competitive importance of species (Roush, 1988). Regardless of the kind of stress, competition is of no importance when the stress leads to death (i.e. Calandrinia when sprayed with 2,4-D; Table 12).

Biomass and species selectivity - Aboveground community biomass decreased with the application of atrazine and 2,4-D, but not with the insecticide malathion. The few reports of phytotoxicity by malathion used higher than recommended doses

(Dennis and Edwards, 1961, 1962). Malathion had little phytotoxic effect when applied at the recommended rates on early successional species (Brown et al., 1987). None of the species Brown et al. (1987) investigated, including Capsella, had significant biomass change. However, in this study the recommended application rate reduced Erodium biomass. In an old field sprayed with diazinon, an organophosphate similar to malathion, a phytotoxic effect on the dominant species, Convolvulus, resulted in other species (Raphanus and Ambrosia) increasing in density and diversity and community biomass increasing (Shure, 1971). In contrast, the application of sevin, a carbamate insecticide, caused no changes in community biomass but reduced litter decomposition and arthropod biomass and numbers (Barrett, 1968). Fungicides also have limited phytotoxicity (Paul et al., 1989). For three of nineteen "weedy" herbaceous plants, including Capsella, fluzilazol reduced growth in a greenhouse (Paul et al., 1989).

Compounds designed to affect plants, such as 2,4-D in wheat fields (Hume, 1987) and the growth retardants maleic hydrazide, mefluidide, and pallobutrazol in pastures (Marshall, 1988), caused reductions in the influence of the dominant species and, therefore, changes in community structure. Furthermore, pesticides in general have selective phytotoxic properties, as demonstrated here with malathion and with others such as diazinon (Shure, 1971) and fluzilazol (Paul et al., 1989). The selective phytotoxicity of insecticides and fungicides is similar to most herbicides, but is less frequent and less severe. Industrial chemicals also have selective phytotoxic properties (Mc Farlane et al., 1990; Pfleeger et al., 1990). The selective phytotoxicity of organic compounds can radically alter the structure of plant

communities depending on the particular chemical involved.

Weed populations in general are greatly affected by herbicides, but most species survive in small numbers (Chancellor, 1979). Species that were severely impacted by atrazine (Stellaria) and 2,4-D (Calandrinia and Erodium) became unimportant in their communities in this experiment, but they were not totally eliminated. Hume (1988) found ten different mechanisms that allowed two species that were sensitive, but dominant in untreated communities, to survive 36 consecutive years of 2,4-D application. This has ecological importance because the few individuals remaining of the former dominant allow the rapid recovery of plant communities following 'disturbance'. This is fundamental to the resiliency of most ecosystems following perturbation.

Removal experiments - The application of selective herbicides to plant communities is similar to the physical removal of plants, a common manipulative technique used on natural plant communities to alter community composition, proportions and densities. As with the physical removal of plants, chemical removal can have the undesirable effect of injury to the remaining plants. Fowler (1981) used both physical (to remove individuals) and chemical (to remove groups) removal on a periodically mowed grassland. While no relationship was found between the ecological role and the taxonomy or morphology of the species, a differentiation was found between C_3 and C_4 species (Fowler, 1981). Although, the current study was limited to winter annuals (C_3 plants), species with basal rosette morphologies were the most consistently competitive species; this contrasts with the findings of Fowler (1981). Pinder (1975) found the removal of dominant species in an old field

community increased the production of subordinate species but not total community production. Similar changes were found in communities treated with atrazine and 2,4-D, with some subordinate species having biomass increases while community biomass generally decreased (Figure 1). In another old field study, community recovery after selective removal was correlated inversely with the cover of the species removed (Allen and Forman, 1976). In the current study, no overall correlation was observed between treatment effects and community recovery as measured by percent cover in communities (Figures 2-4).

Instead of removal, Goldberg (1987) planted Solidago at a variety of different densities and in different species' neighborhoods. This necessitated the removal of some neighborhood plants. The finding that the transplants were inhibited by the presence of neighbors agrees with the results in Table 7, where target biomass increased with increasing neighbor reduction (biomass and number) as long as the treatment was not toxic to the target (2,4-D on Calandrinia) and was toxic to some neighborhood species.

In general, physical and chemical removals led to similar results. However, in some instances the use of herbicides that are painted or sponged on individual plants probably might have fewer subtoxic side effects than removals by sprayed herbicides.

Soil fertility - Any field test to assess phytotoxicity must control environmental heterogeneity. In these experiments, the raised beds were covered with uniformly mixed seed bank soil, with the soil being leveled and initially watered. However, soil fertility was deliberately altered between the two field seasons. The first year

(1988) treatments were fertilized to the manufacturer's recommendation, producing luxuriant plant growth, especially of Stellaria, in the control treatments; plants were so intertwined that the location of the emergence from the soil could not be identified for individuals. The following year no fertilizer was added. This difference allowed comparison of how different nutrient conditions affected community structure and competition. This comparison lacks the necessary control to generate conclusive results due to inter-year environmental variability. However, in a two year field study using annuals, there were no significant changes in the hierarchical structure when resources were not altered (Miller and Werner, 1987). Despite the lack of environmental control, information can be extracted by comparing the control treatments from both years.

Fertilized control treatments had a different species hierarchy than those unfertilized (Figure 5). The most noticeable change was the Stellaria's reduction from the most dominant species to the sixth, based on aboveground biomass. Some species declined as did Stellaria (Veronica and Lamium), others increased (Poa bulbosa, Erodium, and Calandrinia), while others did not change in the hierarchy (Poa annua and Capsella). Similar changes in dominance and composition occurred in old field communities (Bakelaar and Odum, 1978; Tilman, 1984, 1987; Carson and Barrett, 1988; Carson and Pickett, 1990), as well as in mixtures of grasses in culture (Austin, 1982), when nutrients levels were altered.

The data suggested that the variance associated with species biomass increased when soil fertility decreased. A F-test was used to compare the sample

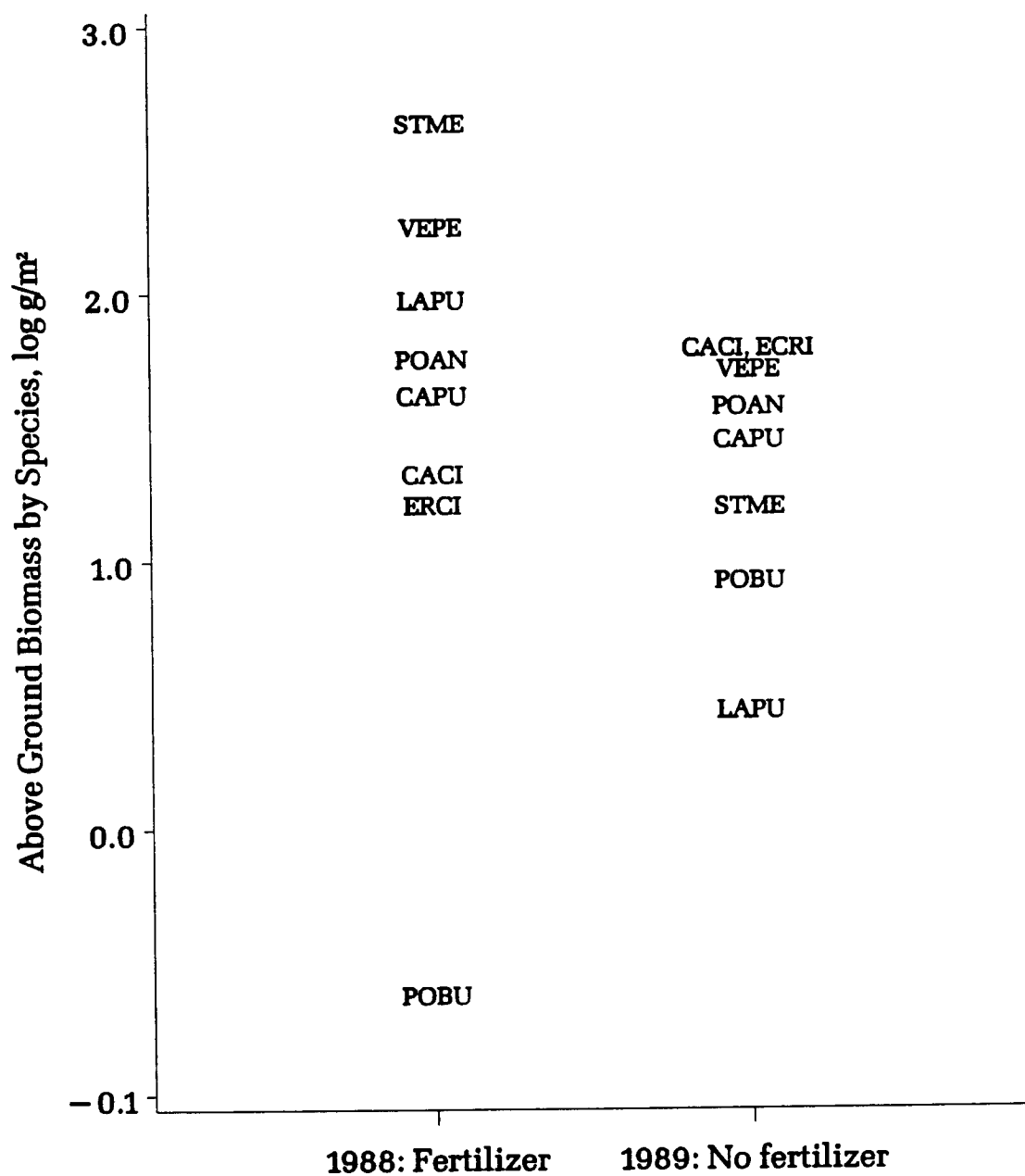


Figure 5. The effect of fertilizer on individual species' aboveground biomass within the control plant communities. The 1988 experiments were fertilized but in 1989 they were not. The data shown here are for only the control treatments for each year. Species codes are defined in Table 2.

variances of each species between years ($N = 3$, $\alpha = .05$). In only two species was there a significant difference, Poa bulbosa and Lamium. Both species were rare and with low biomass, so more variability would be expected with them. Overall, there was insignificant evidence to indicate a difference in biomass variability based on soil fertility.

The fertilized control treatments had more than twice the biomass of the non-fertilized controls (Figure 1). The large shoot mass in fertilized controls probably produced competition for light (asymmetric competition), whereas in the non-fertilized treatments competition was more likely for nutrients (symmetric competition). An indicator of the importance of competition for light is the significance of bare ground in the regression analysis. The fertilized controls had bare ground significant in only one out of eight instances (Tables 8, 9), whereas the unfertilized controls had five of eight significant (Tables 11, 12). If size inequality increased under conditions of asymmetric (light) competition (Weiner and Thomas, 1986), there would be larger variances associated with the fertilized plots, but there was no significant difference between control variances of the two years. Therefore, the apparent asymmetric competition did not lead to larger size inequality.

The optimal soil fertility level for this kind of experiment should be between the two levels used in this experiment. Without a reasonable amount of fertility, the plants would not grow large enough to interact and therefore competition would not be important. The unfertilized treatments had competitive interactions, but not as many as the fertilized treatments. With abundant fertility, the plants were so productive that they became difficult to harvest. The range between luxuriant

growth and insufficient growth is apparently broad and, therefore, should not be difficult to obtain.

TEST METHODOLOGY

The introduction of xenobiotic compounds into the environment has many potential effects and no particular method can test for all possibilities. The methodology described here investigated the effects on biomass and plant interactions of a natural plant community. When a new method is suggested, many questions arise about its adequacy. For this community level test, one must select which species to use, environmental conditions to provide, parameters to measure and analyses to perform. All these factors need to be considered in evaluating its performance.

Test species - Most plant species currently recommended for phytotoxicity testing are agricultural crops (Table 1). Whether agricultural species are adequate surrogates for all terrestrial vascular plants has not been experimentally tested, but it seems unlikely, given the genetic diversity in natural biological systems and the differences in form and function among plant taxa. One attempt to answer this question was to compare phytotoxicity data (EC_{50}) among taxa at the same taxonomic level from a wide variety of published literature (Fletcher et al., 1990). Similarities in toxicity decreased rapidly as taxonomic classification broadened, with similarity high at the generic level and decreasing rapidly thereafter. Most agricultural plants have been selected for characteristics that have little or no selective advantage in natural ecosystems. Most recent crop breeding programs have

unknown effects on tolerance to xenobiotic chemicals, except for genetic engineering of herbicide tolerance into crops. The natural seed bank has the genetic variability lost in most agricultural species and it has taxonomic diversity. Its use was an attempt to make the species selected for phytotoxicity testing more representative of the vegetation actually being impacted by organic chemicals.

The US EPA Office of Pesticide Programs has listed six criteria for indicator or test species (Urban and Cook, 1986: page 14).

The test species should be one which has demonstrated sensitivity to the known effects produced by toxic chemicals;

The dose-response [relations] of the test species to a variety of pesticides [should be known];

The test species should be ecologically significant, occurring naturally in large numbers and in widespread habitats;

The test species should be aesthetically and/or economically important;

The test species should be readily available for test purposes;

The test species should have a life-cycle short enough to permit reasonably short (1 year) life-cycle tests.

The plant community used here meets all these criteria except the second one. The seed banks of disturbed lands are associated with human activity (i.e. farming) and so are readily available. They are composed mainly of widely distributed 'weed' species and are adapted to local environmental and agricultural conditions. The species used in this study were winter annuals but elsewhere these same species grow as summer annuals (Fernald, 1970). Species of disturbed lands have several advantages as test species, including genetic variability, short life cycle, large geographic distribution (in most cases, world wide) and ease of germination

and growth. They also have some disadvantages, including continual seed set, and the lack of perennial species or species with significant storage tissues. The latter two deficiencies could result in overestimating a toxic effect, because storage tissues or dormancy generally have a buffering effect on toxicity. Realistically, it would be difficult to use mature larger perennials in regulatory test protocols, and seedlings of perennials have the disadvantage of not completing their life cycle.

Test parameters - It would be desirable to find the most sensitive parameter indicating change caused by xenobiotics introduced into an ecosystem. Certainly, in most terrestrial ecosystems the structure of the plant community serves as a major determinant of ecosystem dynamics. It would seem important to determine what measures best indicate structural change in plant communities and in some cases the mechanism of that change.

Aboveground biomass data were easy to gather and interpret. Biomass depends on many factors and is generally measured once, eliminating the chance for time trend analyses. There were four patterns shown in the species biomass data from the communities in response to chemical addition. A species' biomass was 1) unaffected, or 2) it decreased, or 3) it increased, or 4) it decreased only at the high concentration. A fifth response was peculiar to malathion, where both the high and low concentrations produced the same biomass reduction (Capsella and Erodium, Figure 1).

Cover values were probably the easiest data to gather and simple graphic techniques were employed to evaluate the data. Cover has been suggested as a better predictor of performance than biomass, especially where light is limiting

(Goldberg and Werner, 1983). Cover of woody neighbors was the best index (of the seven nondestructive measures tried) of interspecific competition on Douglas-fir saplings (Wagner, 1989). Cover value determination was nondestructive so community dynamics could be observed through time (Figures 2-4). This is important, because competition can vary in time (Connell, 1983). Changes did occur in species cover through time, but the impact of the chemical was generally observed by the first sampling and no later than the second (Figures 2-4). Other reasons can account for later changes in cover, such as plant morphology (bolting of Capsella) or senescence (early life cycle completion of Lamium). Two samplings might have been sufficient to draw conclusions about chemical effects on cover because trends changed little between samples one and four (Figures 2-4).

The use of neighborhood analysis produced much greater detail about the chemicals effects on target organisms. The ANOVA results on the neighborhood cover values between treatments at each sampling (Tables 4-6) correlated well with the biomass data (Figure 1). The greater replication allowed with the neighborhood cover estimation produced statistical significance for some trends that had been displayed in the biomass data, but which were not significant. Consider the nonsignificant increase in Calandrinia biomass with higher atrazine concentrations (Figure 1). This became three significantly different responses when measured with neighborhood cover values of both Poa or Calandrinia targets (Table 4). Similar increases in significance using cover happened in 2,4-D treatments and to a lesser extent in malathion treatments.

Regression analysis - Regression analysis was used to investigate changes in species interactions and to help understand the role of competition in forming community structure. While regression analysis is not difficult, it requires many decisions, including whether to use outliers and transformations. These make interpretation more uncertain than the previously discussed methods. The outliers in this experiment were large individuals, as would be expected in a natural plant population, which generally is composed of mainly small individuals with a few large individuals (Harper, 1977). If the large individuals had been removed for the sake of a higher R^2 or better residual plots, the most important reproductive individuals in the community would not have been considered.

The detail from regression analysis may be more than is needed from a regulatory viewpoint, but it added understanding about competition and the consequences of chemical addition. For example, Stellaria, the dominant species in the control treatments in 1988 both by biomass and percent cover, was a significant competitor to Poa only in the second sampling period (Table 8). In contrast, it was a significant competitor in all four sampling periods in the low atrazine treatment, even though it no longer was dominant (Figure 1). Erodium, with low biomass and cover in the atrazine experiment, was a significant competitor in all treatments, in spite of its rarity (Table 8). Using only data on species importance and the changes caused by treatment, the biotic forces structuring the community are likely to be less understood and potentially misinterpreted.

Most regression models used in plant competition studies have their theoretical basis in the reciprocal yield law (Shinozake and Kira, 1956). This

approach generally uses density as the predictor variable (Spitters 1983). However, density may not be an effective measure of biological importance, because it substitutes, among other things, for structure and mass while not explaining that information (Mack and Harper, 1977). Biomass would seem a better parameter. Unfortunately, it can be difficult to measure, particularly in productive neighborhoods (controls, Table 14). Additionally, the measurement is destructive and biomass is more a result than a process or mechanism of competition (Roush and Radosevich, 1985). In any event, using species biomass as a predictor variable gave little new information beyond that from using neighborhood cover values.

The regression models used were full models, retaining species that were not significant. This was done so comparisons between treatments could be made based on the same model. Retaining non-significant species probably caused an overestimation of R^2 , which was used to indicate the importance of competition. The full multiple linear regression model, in all probability, was not the best model (best residual plots) for each treatment or sampling period and it should not be used to compare results outside of this experiment.

Neighborhood size - Some studies using the neighborhood approach have mapped all individuals within the study area (Mack and Harper, 1977; Silander and Pacala, 1985). This approach allows for the flexible manipulation of neighborhood diameters depending on model building results. This study used two sizes of nested quadrats, with results from regression models determining the most significant neighborhood diameter. While mapping the location of individuals allows a range of neighborhood sizes to be considered, it is also expensive and would have been

very difficult due to the physical complexity of the communities, with dense procumbent herbaceous annuals.

Fewer data would be necessary if the most appropriate neighborhood size were known. The regression analysis using cover as the predictor variable in the atrazine experiments had more significant interactions in the 10 cm versus the 20 cm neighborhoods regardless of target species (Poa targets, 34 to 24, Calandrinia targets, 28 to 17). The 2,4-D and malathion experiments had similar results for Calandrinia (27 to 14 and 37 to 32) but Poa had more significant interactions in the 20 cm neighborhoods in the malathion experiment (17 to 29) and the same number in the 2,4-D experiment (21). Between years, the area of influence on Poa may have increased due to the reduction in soil fertility. In the high fertility conditions of the 1988 (atrazine) treatments, the area of influence may have been reduced due to increased competition for light resulting from increased biomass. In contrast, all regressions using biomass as the predictor had the highest number of significant interactions in the 20 cm neighborhoods, regardless of target species, chemical treatment, or response variable (target biomass or height).

This suggests that the area of influence of neighboring plants depends on the parameter measured. Plants rooted in the outer portion of the 20 cm neighborhood could have shoots in the 10 cm neighborhood. This would be very influential when competition for light was important. Conversely, the interpretation of biomass data assumes that the plant is symmetrically distributed around where the shoot emerged and, therefore, it negates the importance of asymmetric above- and belowground plant morphology in resource sequestering. The location where

a plant emerges from the soil may not be the most important factor in the spatial relations between neighboring plants but rather the plant form may be. Werner (1977) concluded that neighborhood diversity of growth forms explained the success of Dipsacus better than abundance of individual species. Many neighborhood models implicitly assume that competition can be completely described in two dimensions, whereas in reality it is a spatial process in which the performance of any individual depends on the three dimensional structure of its canopy and root system in relation to neighbors as well as its distance from them (Firbank and Watkinson, 1987).

In this experiment, cover was a more useful predictor than biomass. Cover measurement was nondestructive and therefore repeatable over time, it was relatively fast, and more interactions were recorded. Biomass measurements could be done only once because they were destructive, were very time consuming, and required the unrealistic assumption that plants were symmetric about the rooting point.

REGULATORY QUESTIONS

The use of multi-species or community level testing raises several concerns. Most important is the economics of using complex field studies, which currently cost as much as a million dollars per avian field test (R. Bennett, US EPA, personal communication). Therefore, this section attempts to determine whether simplification of the procedures used here can produce adequate results for regulatory purposes and whether the assumption that multi-species testing is better than single species tests is valid.

Target species - Two target species were used to determine if the competitive results were target-specific. The target species, Poa and Calandrinia, differed in response to both chemical stress and competition. However, experimental costs would decrease if only one species were used. Obviously, no single species could display the four major patterns of aboveground biomass found in response to increasing chemical treatment (Figure 1). In addition, if a single resistant species were chosen to represent the entire community, the substantial effects on the community could remain undetected. (The only common trait found among consistently competitive species in this experiment was similar growth forms.) The basal rosette species (Capsella, Erodium, and Calandrinia) had similar responses when measured by biomass (Figure 1) and cover (Figures 2-4). And finally, competitive species changed with the chemical used and each target species had its own suite of competitors that also changed. If the objective is to determine only whether competitive interactions change with chemical insult, and not the precise nature of the change, then either target species would be sufficient.

Single species and multi-species toxicity tests - An underlying assumption in the development of this methodology was that multi-species toxicity tests are a better indicator of the ecological consequences of the release of organic chemicals than single species laboratory tests. From an ecological viewpoint this seems reasonable, considering that ecology is the study of the interaction of organisms with their biotic and abiotic environment and the function of environmental toxicology is to determine the effects toxicants have on ecosystems. Unfortunately, terrestrial environmental toxicology has only begun to consider levels of biological organization

higher than single organisms. While this method is an increased level of sophistication over current single species laboratory tests, it does not evaluate cross trophic level interactions such as herbivory or disease that may have significant impacts on plant community structure.

Single species tests have served a useful role and will continue to be useful. They are needed for determining of dose-response relations on survival, reproduction, physiology, biochemistry and behavior of individuals within a particular species (Cairns, 1983). At the same time, they are inadequate for predicting changes in competition, predation, parasitism, community function, ecosystem energy flow and nutrient cycling (Cairns, 1983). In contrast, Kimerle (1986) suggests that the concept of risk assessment using the quotient method (the expected exposure divided by the hazard (LD_{50})) has shown that complicated multi-species data, microcosms, or real-world field studies are not needed to derive useful 'safe' concentrations that protect life. The exposure is determined from monitoring data or more likely predicted from models, whereas the hazard data are derived from single species laboratory test populations (Bascietto et al., 1990). As the ratio approaches one or larger, the probability that an adverse effect will occur increases. The greatest uncertainty is whether what is observed in the laboratory will actually occur in the field, and a safety factor is applied to account for this uncertainty (Bascietto et al., 1990). However, the ratio method also is flawed because it: 1) does not adequately account for effects of incremental [chronic] dosages, 2) cannot be used for estimating indirect effects of toxicants, 3) has an unknown reliability, 4) does not quantify uncertainties and 5) does not adequately account for other ecosystem effects (Bascietto et al.,

1990).

Although Cairns (1983) and Kimerle (1986) agree that reliance on single species testing has allowed no known adverse ecosystem or multi-species effects, they may be unaware of the secondary responses of biological systems produced by chemical treatment (see literature review). Regardless, there is no experimental evidence to indicate with what degree of reliability one may use single species tests to predict responses at higher levels of biological organization (Cairns, 1983). The reason that single species tests have been successful, despite their lack of realism, is because risk assessment results are buffered with application factors to compensate for uncertainties about response thresholds, and exposures are set for the worst possible case (Cairns and Mount, 1990). Additionally, natural systems are remarkably resilient, further buffering the inadequacy of single species testing (Cairns and Mount, 1990). In fact, results from multi-species testing might permit higher levels of toxicants into natural environments than current regulations allow under single species testing.

From this consideration of the literature and these experimental results, it can be concluded that multi-species testing is a necessary addition to environmental toxicology that will add realism and therefore credibility to ecological risk assessments. In this multispecies experiment, some species (Poa spp.) increased in response to higher levels of chemical. This result would not have been determined from a single species test, nor would the change in species interactions. The multi-species method used here takes advantage of laboratory control by having homogeneous soil conditions, emergence time and replication, while at the same

time using naturally occurring plants and climatic conditions. Numerous test systems (especially aquatic) have already been developed to evaluate toxicants in more realistic environments (Cairns and Mount, 1990; Odum, 1984; Hanson and Garton, 1982). These test systems are in most cases as economical as single species tests, although whole ecosystem manipulations probably are not. However, in certain cases whole ecosystem testing may have some advantages (Perry and Troelstrup, 1988), especially in ecosystem restoration (Harris et al., 1990).

The increase in no-till agriculture has dramatically increased the use of herbicides. The new generation of herbicides, the sulfonyl-ureas, have low mammalian toxicities but extreme phytotoxicity, making them less of a human and wildlife hazard and their application at low concentrations decreases the risk of groundwater contamination. This lack of direct mammalian toxicity along with the ability to genetically engineer herbicide resistant crops increases the potential for widespread use and a consequent increase in undesirable modification of non-target plants and communities. A slow alteration of natural plant communities may be occurring now due to the widespread release of chemicals either through direct phytotoxicity (Krahl-Urban et al., 1988) or by the more subtle processes of evolution (Grant, 1972). The probability of unsuspected and probably undesirable change increases with the continual release of organic compounds without valid ecological testing.

CONCLUSIONS

1. A test method was developed for evaluating effects of anthropogenic compounds on plant communities. This field method used species that grow without cultivation in the geographic region of interest and are therefore adapted to local environmental conditions. Environmental heterogeneity common in most field studies was reduced by the use of raised beds and a uniformly mixed soil containing seeds. Synchronous seed germination was enhanced by initial watering and covering the beds. The optimal soil fertility remains to be determined, but it is between the levels used in these experiments.

This method combines the characteristics of laboratory testing (simple, economical, controlled and precise) and the realism of natural field testing, providing a test with the benefits of both. The method may be appropriate for investigating many processes of interest in plant ecotoxicology. Its use in toxicology testing is enhanced by its small size, making it suitable for transport and requiring little waste disposal.

2. All compounds tested, atrazine, 2,4-D and malathion, modified species abundance in the model plant communities. Community productivity significantly decreased when treated with atrazine and 2,4-D, but not with malathion. There were four patterns of response exhibited by individual species: biomass 1) decreased, 2) increased, 3) did not change or 4) decreased at only the high concentration. Erodium biomass equally decreased at both malathion concentrations. While some species were severely reduced in cover and biomass, no species was completely

eliminated from any community.

Communities were simplified and their dominance hierarchy was dramatically altered when exposed to atrazine and 2,4-D and to a lesser extent with malathion. The dominant species were replaced when treated with atrazine. With 2,4-D, the dominant species was not significantly affected but subdominant species were replaced.

3. Treatment with organic compounds altered interspecific competitive relationships. All chemical treatments changed the identity of consistently competitive species and the timing of important competitive interactions, when species importance was measured by the cover surrounding target plants. Ten cm neighborhoods had more indicators of competitive interactions than 20 cm when cover was the parameter measured. However, when biomass was used to quantify influence of neighbors, 20 cm neighborhoods accounted for more competitive interactions than did the 10 cm neighborhoods. Cover was a better measure of competition than biomass, because it was easy to measure, indicated more species interactions and was nondestructive, enabling competitive interactions to be assessed throughout the growing season.

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